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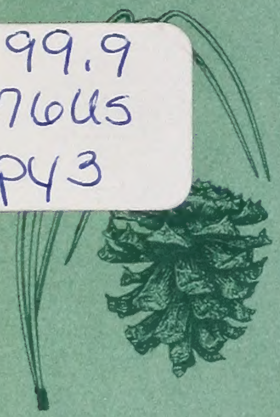

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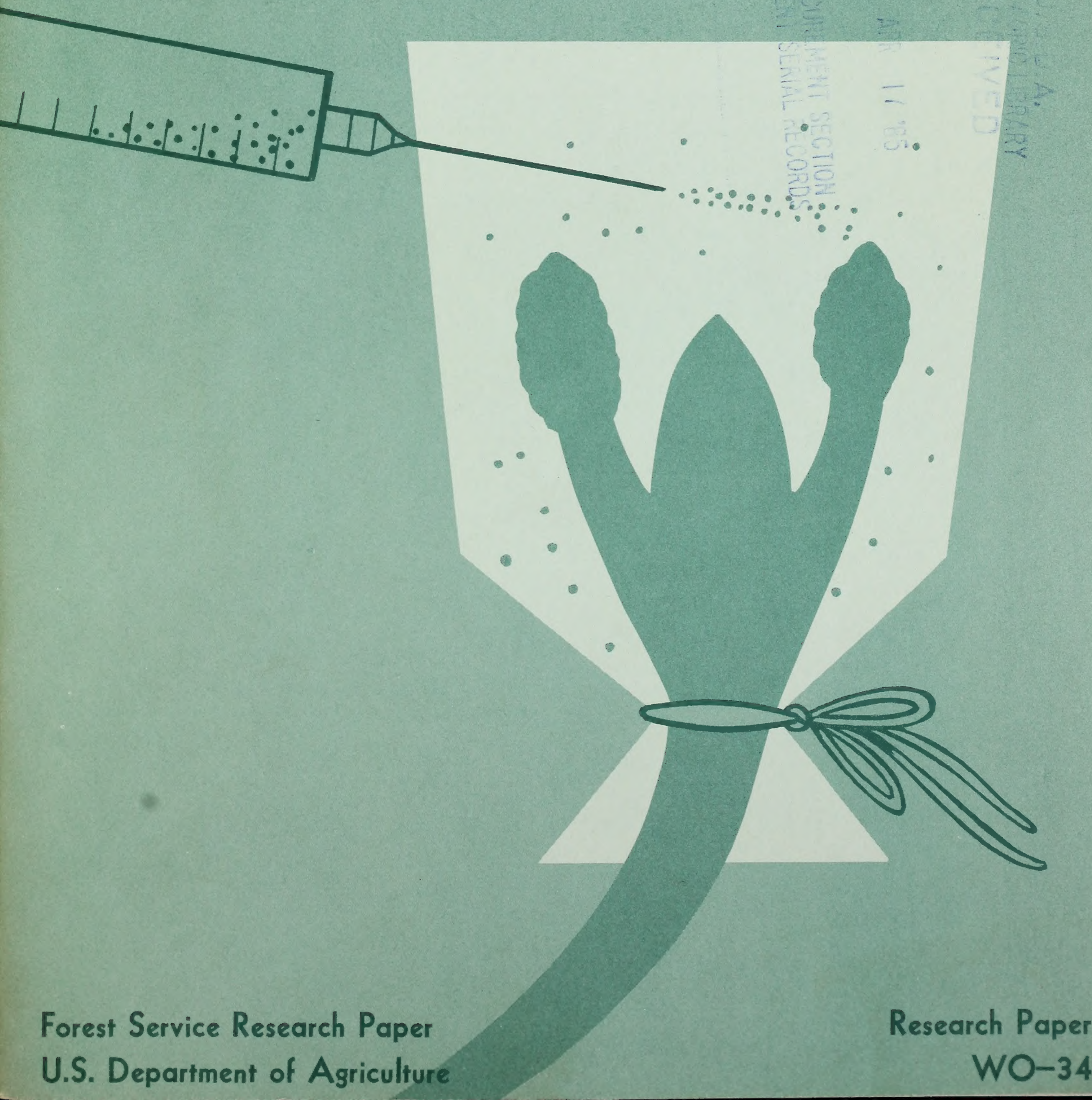

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RESEARCH SUMMARY

The ponderosa pine seed source test of Pikes Peek 1910 is the first forest tree provenance test in the New World. Later replicated experiments confirmed distinct genetic differentiation of geographic and altitudinal variations. The variations appear in a well-defined ecotypic pattern. They distinguish the three toxonomic varieties of ponderosa pine, var. *ponderosa*, var. *scopulorum*, and var. *arizonica*.

Genetic differences have been reported in morphological and physiological traits, including frost resistance, growth initiation, growth cessation, height growth of seedlings to 50-year trees, needle number and color, bud characteristics, stem form, and wood properties.

Natural regeneration is by seed. Seed production is sporadic and good seed years are few and far apart, but seed remains viable after long years of cold storage. Natural vegetation propagation, except root graft, is not reported. Artificial rooting of juvenile materials and grafting of succulent scion on seedling stock are successful.

Techniques of controlled pollination are well developed. Artificial hybridizations have been made in interspecies crosses, interecotypic crosses, back crosses, and trispecies crosses with a number of species and varieties in the subsection *Ponderosae*, and indirectly through *P. jeffreyi* with pines of the subsection *Sabiniana*, the big-cone pine group. The crossability pattern suggests the potentials of hybridization involving numerous species of American and Mexican pines in the long-range breeding program.

Provenance selection is stressed in artificial reforestation and in prairie planting. Tree improvement programs include seedling seed orchard and family selection and stand selection by progency tests. For early production of genetically superior seeds in commercial quantities, the superior trees and the superior stands as recognized by their superior progency performance are maintained as natural seed orchards. Selected through this process, the 12-year height of the half-sib progency families of the best parents are 36 to 50 percent taller than the nonselected local provenance.

GENETICS OF PONDEROSA PINE

Chi-Wu Wang[1]

INTRODUCTION

Pinus ponderosa Laws. is the most widely distributed indigenous pine of the Western Hemisphere. The natural range extends from southern British Columbia to northern Mexico over a distance of approximately 2,200 mi (3,540 km) (Callaham 1960, Critchfield and Little 1966). Economically, it is the most important of North American pines. It has greater timber volume in both growing stock and live sawtimber than any pine species on this continent (Crafts 1958).

Ponderosa pine is polymorphic and genetically variable. The 3-seed source (Arizona, Colorado, and Idaho) provenance test established in 1910 at Pikes Peak (Hayes 1913) and the rangewide 20-seed source experiment (Test Plot No. 162) initiated in 1911 at Priest River in northern Idaho (Kempff 1928) are the earliest provenance test plantations of forest trees in North America. Later, replicated experiments confirmed strong geographic and altitudinal differentiation in ponderosa pine.

Ponderosa pine hybridizes with several pine species and varieties of the subsection *Ponderosae*. On the basis of morphological differences, several variants have been recognized. It is obvious, however, that ponderosa pine belongs to a species complex which includes several distinct and incipient species and varieties with limited genetic restriction of gene exchange.

EVOLUTION AND SUCCESSION

This complex of ponderosa pine and ponderosa pinelike forms was evolved during a long period of the Cenozoic era. Ponderosa pine was represented by fossil species *P. harneyana* in the Eocene circa 40 million years ago in Nevada (Axelrod 1966). This pine, together with the fossil forms of *Abies*, *Picea*, and *Pseudotsuga*, was an element of the Eocene flora found near Jerbidge Mountains (Cooper Basin flora) in Elko County, Nev., south of Twin Falls, Idaho. Wodehouse (1933) observed pollen of *Pinus scopulipites* together with those of two other species of pines from a Middle Eocene strata in northwestern Colorado (Green River flora).

In the western North American continent, ponderosalike pine was widely distributed in the early Tertiary. *P. florissanti* Lesq., a fossil pine, which bore close resemblance to the living ponderosa pine, was first described from the Oligocene bed near Colorado Springs, Colo., and was later reported in the Oligocene in Death Valley (Titsu Canyon), Calif., and in the Miocene near Fallon, Nev. (Lesquereux 1883), MacGinite 1953, Axelrod 1939, 1956 Gaussen 1960). A pine similar to modern ponderosa pine was represented in both the Lower and Upper Seldovian Floras (Miocene-Pliocene) near Anchorage, Alaska (Wolfe *et al* 1966). Fossil *Pinus ponderosa* seed, needles, and cones indistinguishable from the extant species were reported from the Stewart Spring and Fingerrock floras (Miocene) in southwestern Nevada (Wolfe 1964).

The ancestral form of ponderosa pine probably existed in climatic conditions that were milder than those of its living descendant (Chaney *et al* 1944). The range of the ancestral form during the early Tertiary possibly far exceeded the modern range of ponderosa pine in the interior of the continent. The present colonies of ponderosa pine in the Black Hills of South Dakota, in north-central Nebraska, and in western Oklahoma and Texas along the fringe of the woodland-grassland transitional zone possibly represent a once continuous population extending beyond the Rockies.

In the ensuing epochs of the late Miocene and early Pliocene, the Cascade and Sierra Nevada range were formed. This massive uplift brought drastic changes in climate and biota in the Great Basin between the coastal ranges and the Rocky Mountains. The differentiation and speciation within the modern *Pinus ponderosa* complex are possibly related to the increasing continentality, isolation of the inland populations, and its relatively recent migrations (Haller 1965b).

It was suggested that the general trend of expansion was southward from the northwest down to Mexico (Chaney 1936). Apparently the movement took place after mid-Tertiary when the Miocene volcanic activities ceased and the Mexican plateau became available to forest development. The pattern of migration is not clear. The current knowledge is that no fossil pine has yet been found in the Western Hemisphere south of the United States-Mexico border. Shown by their modern distribution, *P. ponderosa* var. *arizonica* Shaw of Arizona and New Mexico is indigenous to Mexico, and *P. ponderosa* var. *stormiae* Martinex and a number of pines of the *pseudostrobus* and *montezumae* groups closely related to *Pinus ponderosa* are all found south of the United States-Mexico border.

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[1] Professor, College of Forestry, Wildlife and Range Sciences, University of Idaho, Moscow, Idaho.

Pollen records indicate that *P. ponderosa* and *P. monticola* persisted during the glacial period in the unglaciated northern Great Basin during the late Pleistocene and into the post-Pleistocene. As the postglacial period progressed, and the climate became warmer and drier, *P. monticola* declined and *P. ponderosa* expanded rapidly (Hansen 1947, 1949).

Superimposed on the general successional trend of ponderosa pine expansion during the xerothermic period were local fluctuations as affected by volcanic activities. Hansen (1942) observed cycles of forest succession on the eastern slope of the Cascades in Oregon which is now occupied by ponderosa pine. The ground was covered by layers of recurrent postglacial pumice deposits from nearby volcanoes. The last pumice fall was 5,000 to 10,000 years ago. After each deposit the forest of ponderosa pine was replaced by *P. contorta*, but the ground was repopulated by *P. ponderosa* during the post-Pleistocene.

PHYLOGENY AND TAXONOMY

Published species of *Pinus* that are closely related to the typical ponderosa pine (*Pinus ponderosa* var. *ponderosa* Laws.) include the following: Apache pine (*P. engelmannii* Carrl.); Arizona ponderosa pine (*P. arizonica* Engelm. *P. ponderosa* var. *arizonica* Shaw); Jeffrey pine, (*P. jeffreyi* Grev. *et*, Balf., *P. ponderosa* var. *jeffreyi* Vasey); Rocky Mountain ponderosa pine, (*P. scopulorum* Lemm., *P. ponderosa* var. *scopulorum* Engelm.); and Washoe pine (*P. washoensis* Mason *et*, Stockwell). In this review, Jeffrey pine and Washoe pine will be considered as distinct species. All the other taxa are recognized as varieties of ponderosa pine.

In addition to the above, two species were recognized in Jeffrey pine (*P. deflexa* Torr. of the high Sierra Nevadas, and *P. peninsularis* Lemm. of northern Baja California), and one variety in Arizona ponderosa pine, (*P. arizonica* var. *stormiae* Mart. of Mexico). Taxonomically, all the above taxa belong to the same subsection, *Ponderosae* Loud, according to Critchfield and Little (1966), and all, except Washoe pine, belong to the same species, *Pinus ponderosa* Laws., according to Shaw (1914). Their phylogenetic relations and their distinctions are of basic interest to genetic studies of ponderosa pine.

Lemmon (1890) suggested that Jeffrey pine is geologically older than ponderosa pine. This view was shared by Dr. Herbert L. Mason (Mirov 1938), who pointed out that the natural range of Jeffrey pine is restricted almost entirely to California and is associated with many endemic plants. On the contrary, ponderosa pine shows distinct geographic variations over an extensive range that stretches far beyond the distribution of Jeffrey pine. The variability of ponderosa pine may be considered as an indication of a species in active process of differentiation.

Biochemical analyses show that ponderosa pine and Jeffrey pine are distinguishable in their oleoresin composition. While there are considerable intraspecies variation among individuals of ponderosa pine and Jeffrey pine, the oleoresin of *P. jeffreyi* contains 88 to 99 percent of heptane, whereas the oleoresin of ponderosa pine contains no heptane (Mirov 1929, 1938; Smith 1964a, 1964b, 1967).

Apache pine (*Pinus engelmanni*) and ponderosa pine were found to be different in several biochemical investigations (Haagen-Smit *et al* 1950, 1951, Iloff and Mirov 1954, Mirov 1954). The turpentine of Apache pine does not contain any delta-3-carene terpene. On the contrary, this turpene was found in large quantities in all samples of ponderosa pine examined, including sources from Arizona, Colorado, Idaho, South Dakota, and Utah.

The hybrid origin of Washoe pine (*P. washoensis*) was indicated by studies of Haller (1959a, 1961) and Mirov (1961). On the basis of morphological variation, Haller concluded that Washoe pine had arisen through hybridization between Jeffrey pine and the Rocky Mountain variety of ponderosa pine. This contention was supported by findings of Smith (1967) that there was a striking similarity between the monoterpene composition of Washoe pine and of individuals of ponderosa pine, particularly *P. ponderosa* var. *scopulorum*.

DISTRIBUTION AND NATURAL ENVIRONMENTS

Ponderosa pine is found chiefly in the mountains between the Pacific and the Rocky Mountains and extends hundreds of miles east of the Divide into Nebraska, Oklahoma, and Texas (fig. 1). It is absent, however, from a large area in the center of its range, which includes nearly all the northern Great Basin, northern Utah, southern and eastern Idaho, western Wyoming, and southwestern Montana. Pleistocene vegetational history supports the interpretation of the Great Basin as a long-term barrier, which antedates late Pleistocene in the differentiation of Pacific and Cordilleram segments of ponderosa pine (Critchfield and Allenbaugh 1969).

Ponderosa pine extends from British Columbia to San Luis Potosi south of the Tropic of Cancer, and from north-central Nebraska to the Pacific Coast over a distance of more than 28° in latitude (approximately 23° 30′ to 51° 30′ N.) and 24° (99° 30′ to 124° W.) in longitude. In the United States it occurs in every State west of the Great Plains. Commercial stands are found in Arizona, California, Colorado, Idaho, Montana, Nebraska, New Mexico, Oregon, South Dakota, Utah, Washington, and Wyoming. Scattered natural stands occur in North Dakota and in the western panhandle of Oklahoma and Pecos County, Jeff Davis County, and Brewster County in western Texas (Read 1969).

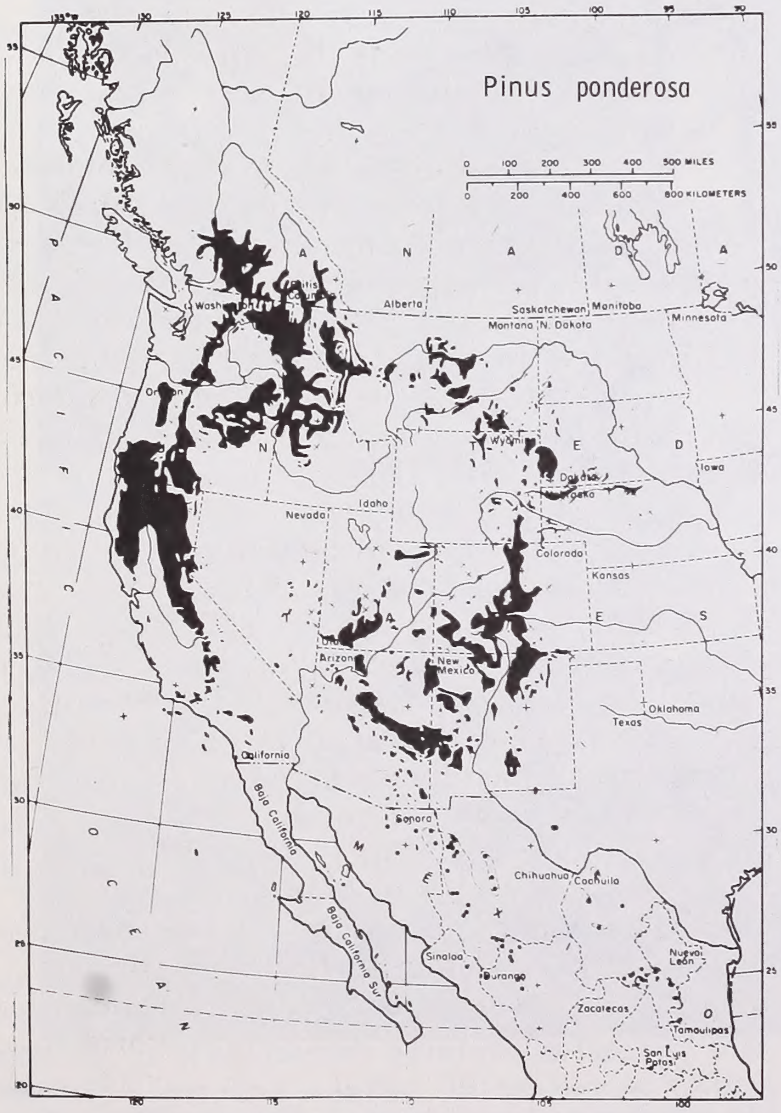

Figure 1.—Geographic distribution of *Pinus ponderosa* Laws. (Critchfield and Little 1966).

In Canada, ponderosa pine is limited to the southern part of British Columbia. It extends along the Fraser, Thompson, Akanagan, and Upper Kootenay Valleys to more than 160 miles (258 km) north of the international border. In Mexico, ponderosa pine is found in eight northern States: Chihauhau, Coahuila, Curango, Nuevo Leon, Sinaloa, Sonora, San Luis Potosi, and Tamaulipas. The altitudinal range is given in the section on Altitudinal Variations.

Throughout the natural range of ponderosa pine, climatic conditions are characterized by great temperature diversities and long rainless periods. In the Pacific coastal region freezing temperatures are not common at lower elevations, but inland, low winter temperatures of −20° to −57° F (−28° to −49° C) have been recorded. This wide range of temperature gradient is conducive to the development of clinal and ecotypic variation in adaptive characters.

With the exception of the ponderosa pine regions of Arizona and New Mexico plateaus, where there are significant summer rains, and the Black Hills of South Dakota and the adjacent plains, where 75 percent of annual precipitation occurs in the growing season, prolonged summer drought is prevalent in most parts of the ponderosa pine region. Baker and Korstian (1931) attributed the large gap in the range of ponderosa pine in the Great Basin region to a deficiency of moisture in the early part of the growing season. The mean annual precipitation is approximately 40 to 50 inches (101 to 127 cm) in the northern Pacific coastal region, 12 to 20 inches (30 to 51 cm) in the ponderosa pine area east of the Continental Divide (Read 1969)[2], and 20 to 25 inches (50.8 to 63.5 cm) in the vast intervening inland and the southern plateaus of Arizona and New Mexico (figs. 2 and 3). In

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[2] Read., R. A. 1969. The distribution of ponderosa pine in Texas. Personal communication.

July and August, however, the mean precipitation is only 1 to 2 inches (3 to 5 cm) in the inland and less than .5 inches in the coastal region.

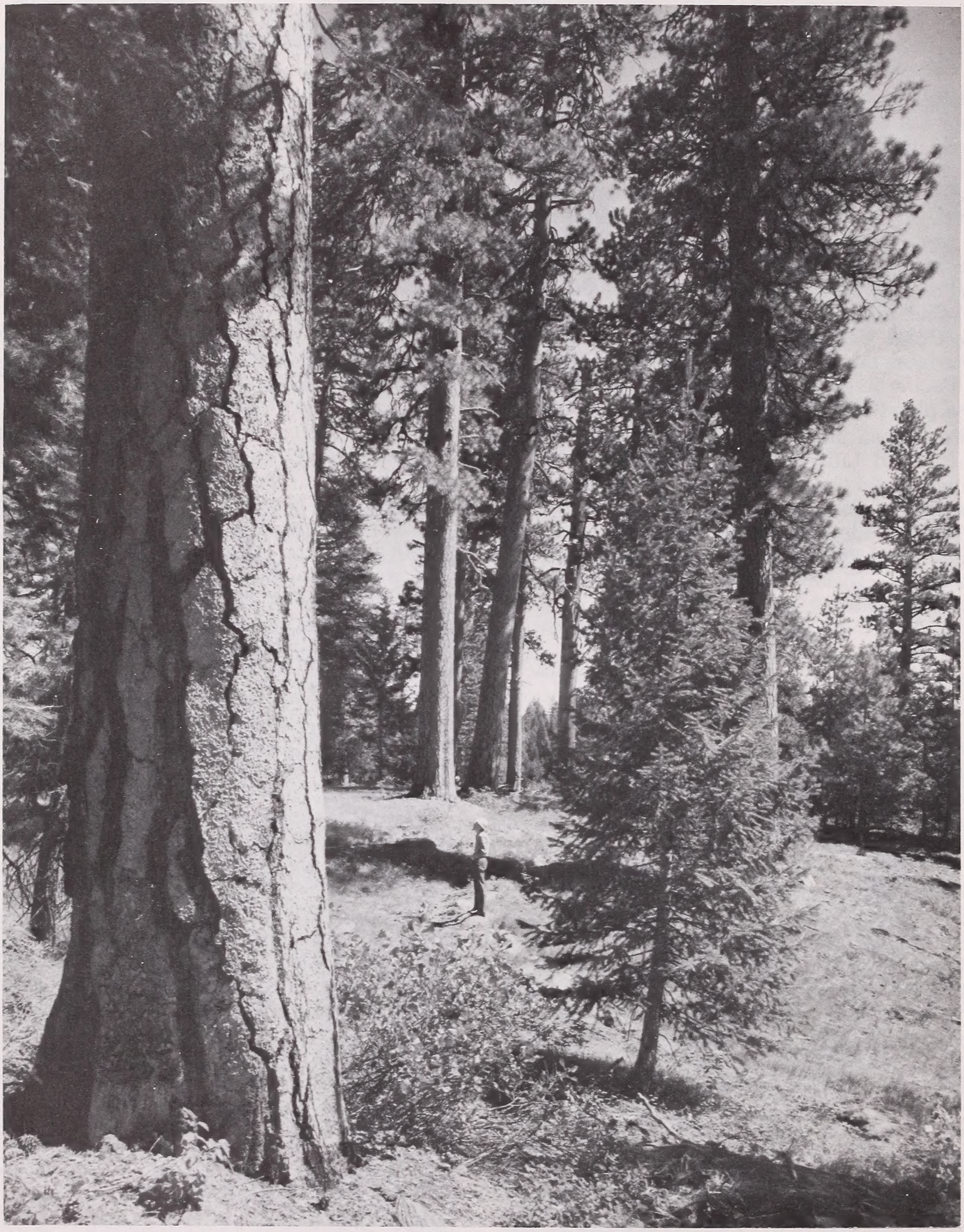

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Figure 2.—A natural stand of ponderosa pine, Boise County, Idaho, where annual precipitation is 25 inches (62 cm) (Boise National Forest, Woodrew Doupe).

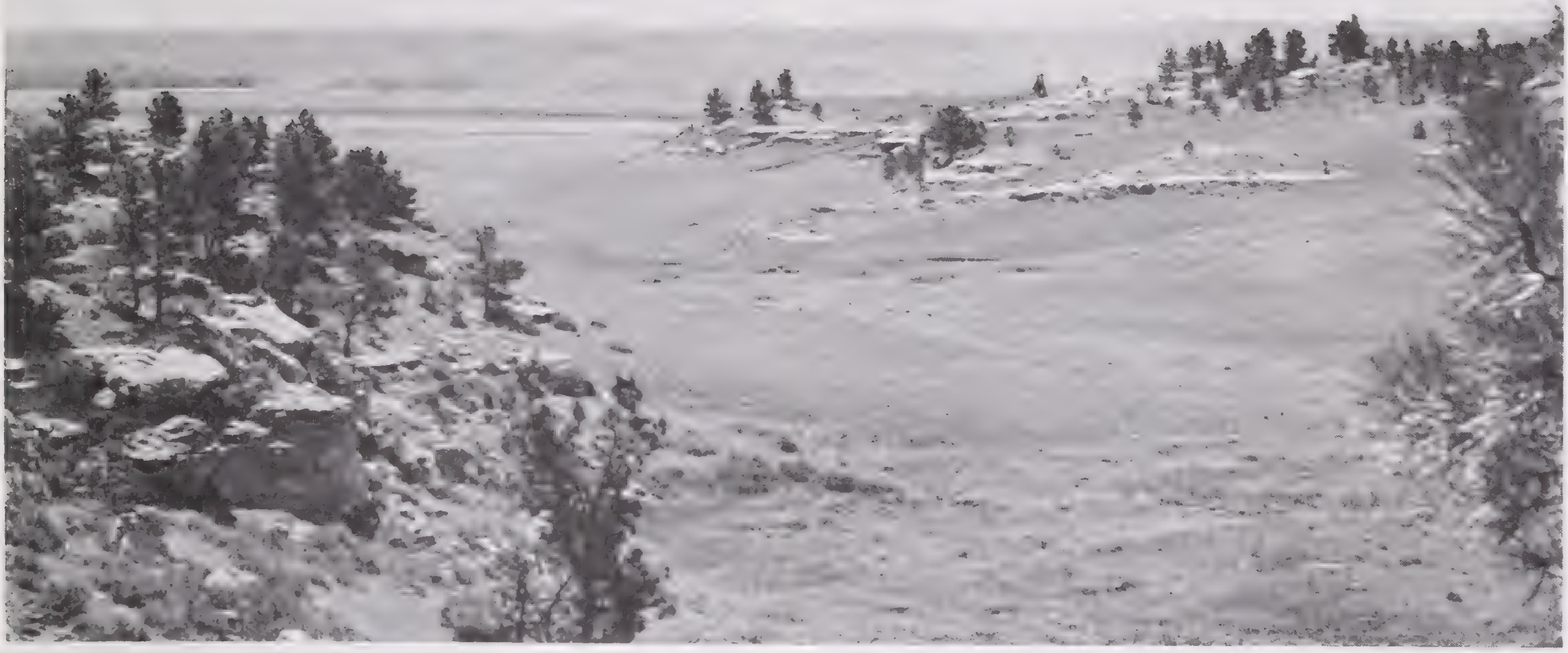

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Figure 3.—An isolated natural stand of ponderosa pine near Potter, Neb., where annual precipitation is normally less than 16 inches (40 cm) (Rocky Mountain Forest and Range Experiment Station, R. A. Read).

The serious fire hazard which exists during the drought period is of special significance to the evolution and survival of this species. Throughout the ponderosa pine region, forest fires occur by the thousands every year. They are ignited mostly by lightning. Although the sporadic fires are highly destructive to established stands, they prepare an ideal seed bed for the successful natural regeneration of ponderosa pine (Herman 1970).

SEXUAL REPRODUCTION

The male and female reproductive organs of ponderosa pine are borne in separate strobili of the same tree. It is common, especially during "off years," that only male strobili are found. However, no differentiation of functionally male and female trees has been reported. Every ponderosa pine larger than 26 inches (66 cm) d.b.h. in a 50-acre (20 ha) natural stand bore some cones during an observed period of 16 years (Fowells and Schubert 1956).

Ponderosa pine is wind pollinated in nature. At the time of pollination in late spring and early summer, megasporophylls (i.e., scales of "conelets"), purplish pink in color, are separated slightly. A transparent exudate is usually visible between the scales. Wind-borne pollen grains discharged in enormous quantities from the microsporangiate strobili become lodged between the scales. The pollinated strobili develop into mature cones 15 to 16 months after pollination or approximately 24 months after the initiation of "flower" primordia.

Strobili Initiation and Embryogeny

The initiation and ontogeny of ovulate strobili were observed in ponderosa pine of California (Gifford and Mirov 1960). In the vicinity of Placerville at elevations of 3,000 ft (914 m), initiation of ovulate strobili occurred during the first 2 weeks of September. While the vegetative shoots and the microsporangiate strobili entered a state of dormancy in winter and the final ontogenetic stages took place the following spring, ovulate strobili continued to grow throughout the late fall and winter. In the early part of May, the presence of young strobili was easily detected by external examination of terminal buds. Oviliferous scale primordia developed into flattened scales subtending on the adaxial surface a pair of ovules consisting of pearly white nucleus tissue. When a pollen grain came in contact with the ovule, it germinated and the pollen tube penetrated the nucellus. The pollen tube ceased to grow in winter and resumed growth in the spring. Fertilization took place nearly a year after pollination.

Over a period of 30 years, Professor John T. Buchholz and his associates (1918, 1922, 1931, 1946) contributed much to our knowledge of ponderosa pine embryogeny. Buchholz and Stiemert (1946) observed that after fertilization the ovulate strobili (conelets) enlarged only slightly during the first growing season, and remain small throughout the ensuing winter. In the following spring, these year-old conelets enlarge rapidly to their full size within a period of 6 weeks. At the time of fertilization, in late June and early July, the cones are fully grown in size though still somewhat succulent. A month after fertilization, the cones have become hard and woody but may remain green for weeks after the seeds are fully matured.

The entire embryogeny and seed development fall into three periods (Buchholz 1946). A 34- to 36-day period of embryo selection, a 10- to 12-day period of embryonic differentiation, and a 40- to 45-day period of seed maturation. During approximately a month following fertilization, the embryos grow very slowly in size. The embryos within each seed are engaged in an intense competition for survival. About 5 weeks after fertilization, the embryo that emerges in a dominant position begins to differentiate. It enlarges rapidly and differentiates all its organs in the 10- to 12-day period. From this point onward embryo elongation subsides and is gradually arrested during the period of seed maturation.

After fertilization, the seed coat hardens in a few days, but there is no appreciable increase in the size of ovules or seed. A seed in which fertilization has failed to take place remains as a full size, empty seed in which the stony seed coat may be as fully developed as in a sound seed.

Multiple seedlings from a single seed were noted from a number of seed lots (Gravatt *et al* 1940). Their occurrence in three-seed lots was 1 out of 5,400. The frequency in 7,598 young seedlings examined was approximately 0.1 percent.

Flower Production and Natural Pollination

In ordinary field conditions ponderosa pine generally begins to produce flowers at the age of about 8 years. The minimum age of staminate flower production observed in ponderosa pine (*Pinus ponderosa* var. *ponderosa*) was 2 years and of pistillate flowers, 4 years. In the Rocky Mountain ponderosa pine (*P. p.* var. *scopulorum*), pistillate flowers were found at the age of 5 years (Righter 1936). The author observed that a 2–0 seedling of Idaho origin produced male and female flowers 2 years after planting. The flowering record of Arizona ponderosa pine (var. *arizonica*) and 32 other pine species planted at the 38° 44′ N. latitude of Placerville, Calif., was analyzed according to the latitude of their natural habitat. It was concluded that the flowering of pine species examined was not affected by photoperiod (Mirov 1956).

There are considerable interregional and intraregional differences in flowering time. Pollination records of the author showed that pollen was collected from Arizona (Flagstaff 6,400 ft, 1,951 m) June 20; coastal Oregon (Corvallis 260 ft, 79 m) May 9; eastern Oregon (Lost Forest 1,420 ft, 433 m) June 10; and northern Idaho (Latah County 2,650 ft, 808 m) generally in the first week of June. In southern Idaho pistillate flowers were receptive in the second week of June in the vicinity of Idaho City (4,200 ft, 1,280 m) but the late blooming trees on Bald Mountain (5,500 ft, 1,676 m) less than 20 miles (32.2 km) from Idaho City, were not receptive until June 25.

These intraregional differences in flowering, apparently common also in other regions, suggest the important role of phenological breeding barriers in genetic differentiation within local populations. Curtis and Lynch (1957) pointed out that there is at least as much intraregional as interregional variation in flowering time and other phenological developments. This observation was based on records taken over 3- to 10-year periods in the five regions where ponderosa pine is found. For further information concerning the date of flowering of ponderosa pine, refer to Roeser (1941), Duffield (1947, 1953), Fowells and Schubert (1956), Curtis and Lynch (1957), and Wang (1970).

The flowering of ponderosa pine in a natural stand in central Colorado was observed over a 10-year period (Roeser 1941). It was found that there was a fairly close synchronization of flower emergence and the last spring frost. During the observed period, the first staminate flowers opened generally from May 22 to June 8, which is about 15 days after the last freezing temperature in spring. The first pistillate flowers generally opened from May 28 to June 23, or approximately 1 to 2 weeks after staminate flowers. In the 10-year period, pistillate flowers were subjected to late frost in only 1 year, but staminate flowers were exposed to late frost in 4 different years.

The 10-year observations indicated that the production of male and female flowers was positively correlated. There was a similar trend in the number of flowers of both sexes produced each year. The average annual production of pistillate flowers in this natural opengrown stand on the .5 acre plot of small to medium-size trees (4 to 17 in, 10 to 43 cm) in the observed period was 2,285 flowers. The maximum number produced in a year was 3,934 flowers.

Successful cone reproduction, however, cannot be predicted by the number of pistillate flowers, except in the case of a very small flower crop, which usually results in cone crop failures. The abundance of pollen supply is one of the most influential factors affecting proper pollination and seed production. In one year of the observed period, when a heavy crop of pistillate flowers (3,142) was accompanied by a light crop of staminate flowers, the cone crop of the year's pollination was less than 1 percent of the total number of pistillate flowers.

Controlled Pollination

The method for artificial pollination of western pines was described in Cumming and Righter (1948) and Duffield (1954). With minor modifications the method has been used satisfactorily in controlled pollination of ponderosa pine. With the exception of the great bulk of the trees and the rough topography where they are usually situated, controlled pollination of ponderosa pine is relatively easy, and good results generally can be expected.

Ponderosa pine pollen can be obtained in quantities with ease at flowering time and can be extracted 2 to 3 weeks before the female flowers become receptive by forcing at room temperature in a humid chamber. Fresh ponderosa pine pollen germinates readily in water within 12 to 24 hours at room temperature. Although germination was not significantly affected by the culture medium after 1 and 3 years of storage, it was significantly affected after 6 and 11 years of storage when a 5 percent sucrose solution produced higher germination than an agar medium (Fechner and Funsch 1966).

Ponderosa pine pollen retains its germination capacity after a long period of storage (Duffield and Callaham 1959), but germination tests of stored pollen on artificial media do not necessarily reflect its ability to produce viable seed. Germinable pollen has been preserved for 11 years (Fechner and Funsch 1966) and 15 years (Stanley *et al* 1960). Stanley (1962) and Stanley and Poostchi (1962) found up to 77 percent germination of ponderosa pine pollen stored 15 years at 5° C (41° F) and 10 percent relative humidity, but only empty seeds were produced in controlled pollination with the stored viable pollen.

The author's records show that 4-year pollen stored at above freezing cold storage temperature in a desiccator produced an average number of approximately 17 seeds per cone. The number of seeds per cone produced in wind-pollinated cones of all trees included in the above controlled pollination is 70.84. There is no significant difference in the number of seeds produced per cone between wind- and control-pollination (Wang 1967). Seed number per cone, seed weight, and germination were little or not affected by artificial self-pollination (Wang 1967, Sorensen and Miles 1974). In seedlings, however, imbreeding depression was 9 percent in first-year survival and 21 percent in first-year seedling height, with the effect on height increasing with age. Frequency of self-pollination seedlings in wind-pollination population was estimated at 11.3 percent. It was recommended that culling of 10–20 percent of a nursery population would appear to be most effective in removing slow-growing self-pollination seedlings and to contribute most to an upgrading of the growth potential of the planting stock (Sorenson and Miles 1974).

Seed Production

The long and tortuous process of embryogeny in ponderosa pine as presented in the previous section explains, in part, the extreme complexity of the problems of seed production. Buchholz and Stiemert (1946) observed that natural pollination of ponderosa pine must be fairly good or the conelets will drop off in the first year, but even if they are retained and enlarged in the second season, many of the ovules may fail to enlarge to form seeds. Presumably these were not pollinated, but this early abortion of half-grown ovules may include some that received pollen which failed in germination. If ovules become full grown, fertilization may still fail in many of them. These would remain as full-size empty seeds. If fertilization actually takes place, there are many embryos that compete with each other for about a month. Finally, those which form cotyledons in the embryos when about a month to 6 weeks old may develop fully as embryos of seeds. Then, and only then, does the viable seed arrive, provided that the season is not too short, as in very high altitudes, or the cones are not damaged by insects, disease, and especially squirrels (Adams 1950, 1955, Squillace 1953, Krugman and Koerber 1969, Shearer and Schmidt 1971).

Of the 10-year annual average of 2,285 pistillate flowers produced in the .5-acre (0.2 ha) natural stand in Colorado, 36 percent survived at the beginning of the second season and 28 percent developed into mature cones (Roeser 1941). In western Montana, 27 percent of the potential cone crop survived the first year of development and only 6 percent reached maturity and shed their seed (Shearer and Schmidt 1971). The losses are attributed to aborted flower buds (5 percent), aborted potential cones (64 percent first year, 6 percent second year), pine squirrels (2 percent first year, 12 percent second year), insects, and unidentified factors (5 percent).

In late July, or about 1 month after fertilization, when the cones were green but had hardened, the seed germination capacity was low. In the period between July 27 and September 5, the germination capacity increased from 0 to 74.1 percent, and the self-extracted seed increased from 0 to 91.6 percent. In the same period, the green weight specific gravity of ponderosa pine cones decreased from 0.92 to 0.74. The specific gravities at the time when the seed appears to reach an acceptable germination and self-extraction capacity were determined to be 0.85 in the northern Rocky Mountains (Maki 1940) and 0.84 in California (Fowells and Schubert 1956). Kerosene and a mixture of half kerosene and half linseed oil were recommended as suitable media for cone maturity tests.

For practical purposes, ponderosa pine begins to bear cones under natural conditions at an age as early as 16 years and continues to produce seed when 350 (Curtis 1955) to 400 (Pearson 1912) years old. Pike's study (1927) of 20- to 200-year-old ponderosa pine in northern Idaho showed that seeds from 121–140 and 141–160 age classes (approximately 14 to 20 inches d.b.h. (36 to 51 cm)) germinated first and had a higher germination percentage (64 and 57 percent, respectively) than younger (27 to 45 percent) and older (43 percent) trees. Pearson's studies (1912) included three age classes: (1) "black jack" or younger ponderosa pine 8 to 14 inches d.b.h. (20 to 36 cm) and approximately less than 140 years old; (2) 140 to 250 years old; and (3) 250 to 400 years old. The percentage of germination of seeds from the above three age classes are 81, 71, and 63 percent, respectively. On the average, the younger pine (140 years or less) produced 1 bu (35 l) of cones per tree, and the older trees (140 to 400 years) 1.8 bu (63 l) per tree. Cones from younger trees produced 1.7 oz (48 g) of seed per pound of dry cones, and those of the older trees produced 1.3 oz (37 g). Although younger trees yield fewer cones per tree when the seed viability and seed yield per cone were taken into consideration, younger trees are better seed producers for their size than the older trees.

Ponderosa pine seed production is sporadic. Good seed years are few and far between. In central Colorado, 2 above-average crop years occurred at 4-year intervals during a 10-year observed period (Roeser 1941). In California, Fowells and Schubert (1956) recorded that 84 percent of the ponderosa pine in a 46.8-acre (18.9 ha) area bore seed crops half of the time during a period of 16 years. They observed that one of the key problems in securing natural regeneration in the pine region of California is that seed crops may be too infrequent to depend on. This is particularly true in the arid inland. Boe (1954) reported that there was one fair or good cone crop and one to six poor crops in western Montana during an observed period of 22 years. East of the Continental Divide in Montana, where var. *scopulorum* is found, there were one to three fair and good cone crops and two to four poor crops during the same period.

No periodicity of seed production has been observed. By means of relating cone crop and temperature records during 1926 to 1950, a temperature hypothesis for flower-cone prediction was developed (Maguire 1956): whenever the average monthly temperatures for April and May are considerably above normal, ponderosa pine trees will flower in abundance the following spring, with the subsequent good cone crop potential in the fall of the following year. Conversely, whenever the temperatures are below normal, few flowers will appear the following year.

VEGETATIVE PROPAGATION

In nature, ponderosa pine is reproduced by seed. Natural propagation by vegetative means has not been observed. Lanner (1961), however, reported several cases of natural root grafts in ponderosa pine, and experimental propagation by grafting, rooting, budding, air-layering, and inarching has been made with considerable success. The methods used in vegetative propagation of ponderosa pine was described in Mirov (1940, 1944), Mowat and Silen (1957), and Parks (1969, 1974).

Ponderosa pine stumps were found alive and growing for a number of years after the removal of their stems by thinning of windfall (Lanner 1961). This phenomenon of "living stumps" has been noted in many tree species (Pemberton 1920, Graham and Borman 1966, Stone 1974) and is known to be produced by root grafts between trees. The cambium of the grated stump continues to add increments of wood and bark. The wood of the living shell gradually differentiates into heartwood and sapwood outside the heartwood and sapwood of the original stump. Of the five ponderosa pine living stumps examined in the Sierra Nevadas, the age at which the trees were felled and the stump growth initiated was between 55 to 75 years; the stumps had been growing at the time of observation for 12 to 30 years.

In vitro culture of ponderosa pine embryo was reported by Howe (1962). Normal seedlings were produced from excised postgerminal embryos on a nutrient agar medium to which auxins in varying concentrations had been added. The auxins included in the test were naphthalene-acetic acid, indole-butyric acid, 2.4-dichlorophenoxyacetic acid, gibberellic acid, and indole-propionic acid. The seedlings were transplanted in quartz sand and later to soil where good growth and development continued.

Four types of grafts and budding techniques were included in a test of vegetative propagation of ponderosa pine (Mowat and Silen 1957). The grafts were made on side branches of 6-year-old ponderosa pine planted in the nursery with fresh cut scion, which was immediately grafted back to the same branch. No significant difference was found among grafts with succulent materials made in mid-June and those with dormant materials made in mid-April. Cleft grafts were statistically significantly better than whip grafts, patch grafts, and bottle grafts. More than half of the cleft grafts using dormant materials and almost three-quarters of those using succulent materials were living at the end of the first season. Whip graft and patch graft methods gave similar results of 21 percent successful union with dormant materials. Bottle grafts, which were thought to have the best chance of success, were a complete failure and were the most costly and time consuming of the methods tested. The bottles needed refilling and mold-control. Budding produced a few living shoots. However, the graft unions were formed chiefly with stembark and seemed very insecure (Mowat and Silen 1957).

In field grafting, succulent scion is better than dormant scion for the California Region. The first-year percentage of take of the California tree improvement project from 10 to 40 percent using dormant scions, to 65 percent using succulent scions (Parks 1969). The "succulent graft" method, which involves the grafting of current growth of the scion into current growth of the root stock, was found to be more successful than the "wood graft" method, which involves the grafting of last year's growth of the scion, dormant or actively growing, into last year's growth on the root stock in field grafting of California ponderosa pine. Graft take was 76 percent with succulent grafts and 38 percent with wood grafts (Park 1974).

For experimental purposes grafting is a valuable method in the preservation and propagation of older trees. Young shoots of several very old ponderosa pine were successfully grafted on 3-year-old ponderosa pine and Jeffrey pine transplants. The grafts were made in April both in the greenhouse and in the nursery (Mirov 1940). Successful ponderosa pine grafts were made in needle-bundle grafting, approach grafting (inarching), and interspecific grafting with other pine species (Mirov 1940). In the interspecific grafting, ponderosa pine was grafted with several pine species of both the white pine and the hard pine subgenera. Cleft graft method was used with 1-year-old seedlings grafted on 1-year-old transplants. Successful graft unions were obtained with ponderosa pine scion on stock of *P. attenuata* (knobcone pine) and *P. halepensis* (allepo pine of the Mediterranean), and with scion of Haploxylon (white) pines (*P. albicaulis*, *P. lambertiana*, and *P. monophylla*) and Diploxylon (hard) pines (*P. attenuata*, *P. banksiana*, *P. caribaea*, *P. coulteri*, *P. glabra*, *P. halepensis*, *P. leiophylla*, *P. radiata*, *P. sabiniana*, and *P. torreyana*) on ponderosa pine stock.

Curtis and Lynch (1957) reported two instances of induced root formation of ponderosa pine branches by air-layering. Rooting of ponderosa pine cuttings was reported by Mirov

(1938, 1944) and summarized in Thimann and Behnke-Rogers (1950). Experiments were made under combinations of different treatments (indole-acetic acid, indole-butyric acid, warm water treatment), different propagation bed temperatures (cold frame at approximately 40° F, 5° C, and hot bed at 70° to 75° F, 21° to 24° C), and different rooting media (fine sand, coarse sand, and sand-peat sand-muck mixtures) with cuttings taken from 4-, 5-, and 30-year-old ponderosa pine. Results showed that the rooting capacity of ponderosa pine decreases with age. The percentage of rooted cuttings taken from 30-year-old trees was 6 percent and that from 4-year-old cuttings under similar conditions was 36 to 68 percent. Warm water soaking of cuttings before installation in the propagation beds produced no consistent results. Treatment with indole-butyric acid produced the best result in the experiment, with 5-year-old ponderosa pine cuttings at the end of 11 weeks and 4-year-old cuttings at the end of 3 months. Indole-butyric acid seemed to accelerate development of the roots. Six months after the beginning of the experiment, however, there was no significant difference between the indole-butyric acid treated 4-year-old materials and the nontreated control. Bottom heat of the coarse sand rooting medium produced far better results than the chemical treatment.

GENETICS AND BREEDING

Karyotype and Mutation

Somatic chromosomes of ponderosa pine endosperm tissue were studied by Sax and Sax (1933). Chromosomes of ponderosa pine were found to be clearly defined and very similar to those of 13 other *Pinus* species included in this study. The haploid chromosome number is 12. In ponderosa pine, one of the 12 chromosomes is somewhat heterobrachial, and the others have approximately median fiber attachments (fig. 4).

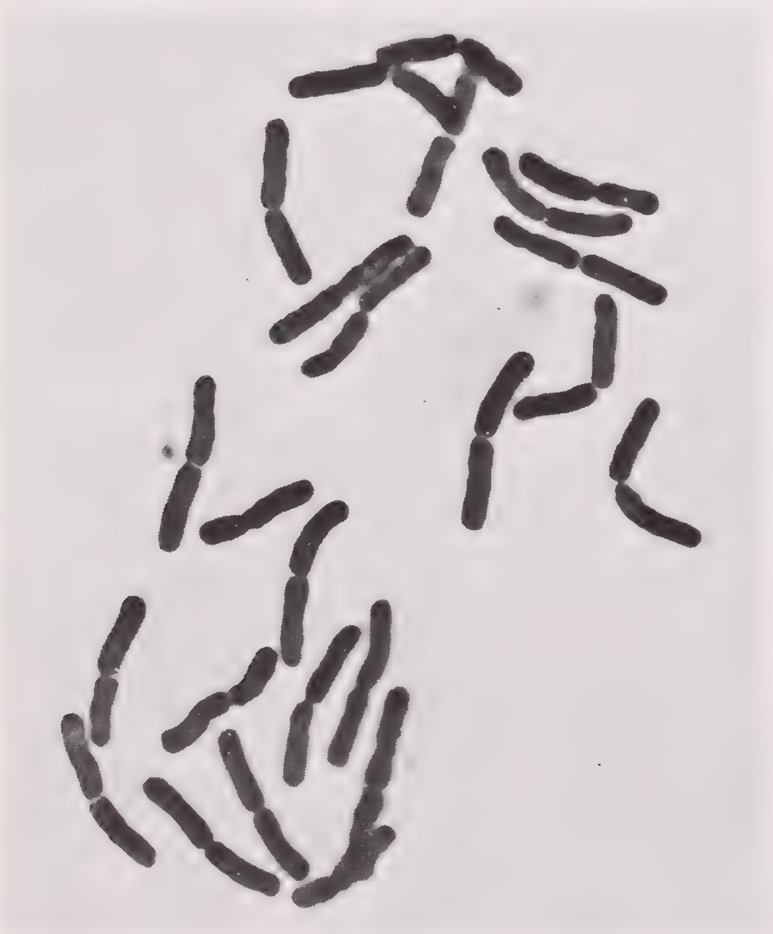
F–524985

Figure 4.—Chromosomes of *Pinus ponderosa,* 2 n = 24 (1225 x). Metaphase chromosomes from acetocarmine preparations of root-tip meristems (L. C. Saylor 1972).

The basic karyotype of ponderosa pine observed from root tip materials (Mehra and Khoshoo 1956) agrees with the endosperm studies. The diploid chromosome number of *Pinus ponderosa* and 11 other pine species investigated is 24. The chromosomes have either a median or submedian centromere. The various species differ in number of secondary constrictions and their locations. No secondary constriction was found in ponderosa pine chromosomes.

Of the 17 species of *Ponderosae* examined, Saylor (1972) found that although there were similarities among closely related species in the subsection, there was no general pattern for the entire subsection. In its karyotype, *P. jeffreyi* has certain features that resemble both *P. coulteri* and *P. ponderosa*, but there is a tendency to favor the latter. Chromosome and nuclear behavior of meiotic pollen mother cells of ponderosa pine are regular. The frequency of various irregularities is low in ponderosa pine and in the hybrid *P. ponderosa* x *engelmannii* but appears higher in precocious disjunction (7.4 to 18.7 percent) and in unpaired chromosomes (4.5 to 11.0 percent) among the hybrids of *P. jeffreyi* x *ponderosa* and *P. ponderosa* x *montegumae* (Saylor and Smith 1966).

Natural polyploidy has not been observed in ponderosa pine. Artificially induced polyploid ponderosa pine seedlings were obtained by colchicine treatment (Mirov and Stockwell 1939). Stratified seeds (5° C, 3 months) treated with a 0.2 percent colchicine solution for 5 days produced a small percentage of abnormal seedlings. The development of the treated seed was delayed as compared with normal seed. The seedlings were weak, with swollen crowns and clublike cotyledons. Microscopic examination showed that the chromosome number varied from 24 to ca. 96 in multiples of 12. Spindle formation was inhibited in some cells, and formation of cell walls was lacking or was vestigial and ineffective. Mirov (1967) reported that pine chromosomes are also resistant to the action of X-rays for inducing mutation. Polyploidy probably has not played an important role in the evolution of *Pinus* (Mehra and Khoshoo 1956). The rarity or absence of natural polyploids and the difficulty in artificial polyploidy induction show the extreme stability in pine chromosomes and their resistance to change.

Early Provenance Tests

Provenance studies have contributed much to our knowledge of the pattern of natural variation of the species. The 1910 three-seed source (Arizona, Colorado, Idaho) test plantations at Pikes Peak, Colo. (Hayes 1913), and the 1911–17 rangewide 20-seed source test plantation of Priest River, Idaho (Kempff 1928, Weidman 1939, Squillace and Silen 1962, Steinhoff 1970), are the earliest provenance tests of forest trees conducted in the Western Hemisphere. They are not replicated, but they did demonstrate distinct differences in morphological characters and survival among different geographic population samples planted in a general area.

Geographic differences of ponderosa pine were also observed in other early nonreplicated provenance tests in Colorado (10-seed source, Black Hill to Colorado, Roeser 1926, Bates 1927); Fort Valley, Ariz. (Schreiner 1937, Pearson 1950, Larson 1966); Nebraska (Higgins 1927); Oregon and Washington (10-seed source, 6-site, Munger 1947, Squillace and Silen 1962). Bates (1927) reported possible varietal differences in preferential animal browsing. The Black Hills provenance was heavily browsed, but other sources were untouched. Records of deer, rabbit, and porcupine damage in plantations of the 1928 10-seed source provenance test in Oregon and Washington (Squillace and Silen 1962) strongly suggest genetic differences among progenies in susceptibility to browsing. Indigenous Nebraska seed sources were found to be less susceptible to tip moth in Nebraska (Higgins 1927).

Cold Resistance

In nature, ponderosa pine is known to be able to survive low winter temperatures of −65° C (−85° F) (Mirov 1967), although, there is a wide range of geographic variation in cold resistance. Severe to fatal frost injuries in the different seed sources were among the most obvious evidences of genetic variation in ponderosa pine observed in the early provenance tests.

In a seed source test of Pikes Peak, Colo., Roeser observed that trees of California and Oregon origins failed from frost damage, while those of local and other sources survived (Squillace and Silen 1962). Pearson (1931) reported that first-year seedlings of ponderosa pine of Sierra National Forest origin planted near Flagstaff, Ariz., were killed by a November frost, whereas seedlings from several other western States planted in the same locality were not injured. The Sierra seed source was from the western slope of the Sierra Nevadas in California, and the November frost temperatures near Flagstaff were probably not lower than −4° F (−20° C) (Haller 1961).

In 2-year-old seedlings, Wells (1964a) observed sharp ecotypic distinctions in cold injury among 298 individual tree progenies planted in Michigan. All progenies of California origin sustained severe to very severe injury, but practically no progeny of the Northern Inland ecotype (eastern Montana, South Dakota, Nebraska) and the Central Interior ecotype (Colorado, Utah, northern New Mexico) suffered any frost damage. Only light to intermediate cold injury was observed in progenies of the Northern Plateau and Southern Interior ecotypes. At 8-year stage, trees of Arizona-New Mexico origins sustained slight winter injury, and the Oregon-California trees sustained severe winter injury in three test plantations in southern Michigan (Wright *et al* 1969).

In 1925, the 20-seed source ponderosa pine plantation of Priest River, Idaho (elevation 2,380 ft, 725 m), experienced a precipitous drop of temperature of 57° to 12° F (14° to −24° C) in 20 hours. All trees of the Shasta, Calif. (elevation 4,000 ft, 1,219 m), origin were killed by frost, but none of Lolo, Mont., origin trees was damaged. Trees of Black Hill, S. Dak., and Bitterroot, Mont. (4,000 ft, 1,219 m), origins showed only very light injury (2.3–2.8 percent). Trees of Coconino, Ariz.; Pecos, N. Mex.; and Siskayou, Oreg., origins were severely frost damaged. Trees of other geographic origins showed only light to intermediate frost damage

(Kempff 1928). The pattern of genetic variation in cold resistance of the 10- to 15-year-old trees is essentially similar to that of 2-year-old seedlings.

Altitudinal Variations

The altitudinal origin of seed sources is one of the most important factors in a selective breeding program, especially for a species with wide altitudinal range. The altitudinal range of ponderosa pine as a whole is from sea level to 10,300 ft (3,139 m) (Shaw 1914, Sudworth 1917, Mirov 1967). Within the Pacific Northwest, it is found from sea level to 6,200 ft (1,890 m) in British Columbia and Washington, and from sea level to 7,000 ft (2,134 m) in Oregon. The altitudinal belt tends to become increasingly higher toward the south. In northern California, the range is 300 to 7,000 ft (91 to 2,134 m) and in southern California it is 4,000 to 9,000 ft (1,219 to 2,743 m). The aspect of mountain range also has considerable influence on altitudinal distribution. Haller (1962) observed that on the western slope of the central Sierra Nevadas, ponderosa pine is mainly found between 3,000 to 6,000 ft (914 to 1,829 m), but on the eastern desert-facing slope it is found between 5,000 and 6,500 ft (1,524 to 1,981 m), as shown in the following tabulation:

Location	*Altitudinal range of ponderosa pine, in feet (meters)*
Idaho	1,000–7,00 (305–2,134)
Montana	2,800–6,000 (853–1,829)
Nebraska	
Dawes County	3,600–4,360 (1,097–1,329)
Keyapaha County	2,100–2,310 (640–704)
North Dakota	
Billings County	2,150 (655)
South Dakota	3,300–6,000 (1,006–1,829)
Utah	
Kane County	5,250–8,170 (1,600–2,490)
Duchesne County	8,000–8,600 (2,438–2,621)
Wyoming	
Crook County	4,550 (1,387)
Johnson County	7,055 (2,150)

Location	*Altitudinal range of Arizona variety of ponderosa pine, in feet (meters)*[3]
Arizona	
Coconino County	4,770–8,400 (1,454–2,560)
Southern Arizona	5,900–8,000 (1,789–2,438)
Mexico	6,200–8,300 (1,890–2,530)
New Mexico	
Otero County	6,000–8,840 (1,829–2,694)

In general, ponderosa pine forests of the Rocky Mountains are found between 4,500 and 8,600 ft (1,372 and 2,621 m), but in the southern Rockies they may reach as high as 9,600 ft (2,926 m).

In a preliminary report of an extensive progeny test of 765 open-pollinated progenies, Austin (1932) noted that the most interesting general tendency observed in the test was that in the Sierra Nevadas, at least, vigor seemed to decrease markedly with increase in elevation. Seeds from 89 trees of Austin's seed collection were test planted at three elevations in the Sierra Nevadas. The seeds were collected from parent trees growing along an altitudinal transect from 125 to 6,919 ft (38 to 2,109 m) on the western slope of the Sierra Nevadas. The three planting sites were 960, 2,730 and 5,650 ft (293, 832, and 1,722 m) above sea level. The result showed a curvilinear relation of progeny growth with altitude of seed origin.

At 12 years, progeny from midelevation parents grew best regardless of the elevation of planting. The general trend, with the exception of the lowest elevation sources, is that trees from high elevations tend to grow more slowly than trees from low elevations (Mirov *et al* 1952). This general elevational trend was also observed in 1-year and 5-year seedlings and in 20-year trees raised from the same seed lots planted in the North Coast Range of California (1,830 ft, 558 m) (Callaham and Metcalf 1959).

At 20 years, the height growth in the low- (960 ft, 293 m) and midelevation (2,730 ft, 831 m) plantations maintained similar elevational trends as observed in the 12-year stage. But in the high-elevation (5,650 ft, 1,722 m) plantation, the influence of seed source on height had changed (Callaham and Liddicoet 1961). Height growth of all sources started leveling off, and trees from high-elevation sources had caught up to those from the lower elevation seed sources. Trees of lower elevation sources planted in the high-elevation (5,650 ft, 1,722 m) plantation sustained the most serious stem and leader damage. The damage may have been a significant factor in reducing height superiority of the lower elevation sources.

At 29 years, progeny from midelevation parents continued to rank tallest in all plantations, but are challenged at the high-elevation site by progenies from high-elevation parents. At low and midelevation sites, tree heights and diameters of progenies from high-elevation parents were the shortest, those from the low-elevation parents intermediate, and those from midelevation seed parents tallest. At the high-elevation site, tree from mid- and high-elevation sources grow equally well, whereas trees from low-elevation parents showed poorest growth. The variation associated with elevation zone of parent trees accounted for 8 percent of the total experimental variation. About 9 percent of the total was attributed to the interaction between parent tree elevation zones and plantations (Conkle 1973).

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[3] Shaw 1914, Sudworth 1917, Little 1950, Curtis and Lynch 1957, Harlow and Harrar 1958, Mirov 1967, and Wang 1976).

Time trend in height growth of the midelevation plantation (Conkle 1973) was analyzed from ages 3 to 29 (Namkoong and Conkle 1976). The materials included 71 families in seven elevation zones of 1,000 ft (304.8 m) each, with midpoints from 500 to 6,500 ft (152.4 to 1,981.2 m). The general growth curve was sigmoid and similar for each zone's mean curves, for each family's mean curves, and for all individual tree curves. But the pattern varied significantly by zone and family within zone in slope and time of phase change. A variance component estimate shows that zonal differences are large. Magnitude of zone variance increased from the 3rd to the 20th year as a ratio of total variance and as a ratio of mean height.

Genetic and environmental effects on wood specific gravity were found in the 29-year-old progenies from different elevation sources. Wood specific gravity decreased with increasing elevation of seed parent. This decrease occurred regardless of whether the trees were grown at the low- (960 ft, 293 m) mid- (2,730 ft, 831 m) or high- (5,650 ft, 1,722 m) elevation plantations. The decrease was slightly more pronounced for seed sources growing in the high-elevation plantation. Elevation of seed sources accounted for 9.8 (inner core) and 12.3 (outer core) percent of the total variation. Plantations differed significantly in their outer core specific gravities. All genotypes had lower specific gravities in the high-elevation plantation than in the mid- and low-elevation plantations. Thus, high-elevation parents tended to produce offspring of low specific gravity, regardless of site elevation, and all seed sources tended to produce less dense wood when grown at higher elevations. The results indicated that for optimum production of ponderosa pine under similar California conditions, midelevation sources outplanted at about 3,000 ft (914 m) should give the combination of the highest volume yield of higher specific gravity (Echols and Conkle 1971). In tracherd length, the influence of elevation of seed parents was found to be not significant. Plantation location was significant, but interaction between progeny and location was not. Regardless of elevation of parent source, trees planted at high elevations produced shorter tracherds than those planted at either mid or low elevations. Although genetic differences were not obvious in this study, the occurrence of individual trees with longer tracherds at all three sites suggests possibilities of genetic improvement by selection (Echols 1973).

In 1937, at the California Institute of Forest Genetics, Lloyd Austin started a comprehensive progeny test of 627 wind-pollinated progenies of El Dorado County, Calif. The seed trees were selected along an altitudinal transect of the Sierra Nevadas. They represented a distribution of 7,000 feet (2,134 m) in elevation (Day and Austin 1939). Fifteen-year height growth and its relationship with seed tree elevations, seed size, germination time, and second-year growth of 81 of the progenies that were outplanted in a test plantation were analyzed and reported by Callaham and Hasel (1958, 1961). Multiple regression analysis indicated that height growths in the second year were related to seed size, germination time, elevation of the seed source, and crop year of the seed. Greatest second-year growth was found in large-seeded, fast-germinating, low-elevation progenies. Fifty percent of the variation in second-year height growth was associated with variations in these variables. Seed size and germination time were in turn related to elevation of the seed source. Seed from lower elevations was larger and germinated faster than seed from higher elevations.

However, height growth at 15 years was significantly associated only with height growth in the second year and with elevation of the seed source and elevation squared. Progenies growing tallest in the second year and originating from midelevation (2,000 to 3,000 ft, 610 to 914 m) sources were tallest at 15 years. Seed size, germination time, and crop year all had lost their significant influence on 15-year height growth. About 39 percent of the variation in 15-year height could be attributed to inheritable genetic differences among progenies.

The most important result of this study was the relationship established between the juvenile and later growth of progenies. This study indicates that seed trees producing relatively large seed that germinates rapidly tend to produce taller 2-year seedlings. These criteria, however, cannot be used to select the tallest progenies at 15 years. To select 15-year progenies that are prospectively best, select in the nursery on the basis of second-year height growth in combination with altitudinal origin of the seed tree.

The altitudinal race experiments of ponderosa pine showed the presence of definite inheritable differences in height and diameter growth associated with the elevation of the seed tree. They showed also the presence of genetic differences in growth between progenies of the same general elevations. The result suggests that for the selective breeding of a wide-ranging species with distinct altitudinal differentiation such as ponderosa pine, superior progenies can be effectively obtained from selection within the optimum altitudinal zone of the best geographic sources.

Rangewide Provenance Tests

Differences in growth among the 20 population samples in the 1911–17 rangewide ponderosa pine provenance test plantation at Priest River, Idaho, were reported by Kempff (1928), Weidman (1939), Squillace and Silen (1962), and Steinhoff (1970). The trees of different geographic origin showed striking differences in several foliage characteristics (Weidman 1939). Weidman recognized four races of ponderosa pine, which occur on the coast north of California; in western Montana, Idaho, and the inland portions of Washington and Oregon; in Arizona, New Mexico, southern Utah, and southeastern Colorado, and east of the Continental Divide as far south as southern Colorado and west of the Continental Divide in northwestern Colorado and northern Utah. Correlation between height at age 50 and height at early ages did not become consistent within as well as among the provenances until age 20 (Steinhoff 1974). Within most provenances there was a regular increase in the correlation coefficient with increasing age; however, for one provenance, the correlations remained nearly constant at the 0.90 to 0.95 level.

Early results were reported by Munger (1947) of the 1928 10-seed source, 6-test site, pondersa pine provenance test plantations in Oregon and Washington. The 30-year data from five existing plantations, analyzed by Squillace and Silen (1962), gave conclusive evidence of the presence of genetic differences among trees of different geographic sources in height growth, diameter growth, volume growth, stem form, needle length, animal damage, and survival. In initiation of leader growth, provenance differences were observed in both the 10-seed source test (Squillace and Silen 1962) and the 20-seed source test (Hanover 1963). No significant difference was observed in cambium activities of 14 of the 20 sources in the Priest River plantation (Daubenmire 1950). They varied considerably from tree to tree within individual provenances.

The Michigan rangewide ponderosa pine provenance test included 298 open pollinated progenies from 60 different stands in 12 western States and British Columbia. The major division between the typical variety of ponderosa, *P. p.* var. *ponderosa*, of the Pacific Coast and the Rocky Mountain variety, *P. p.* var. *scopulorum*, was verified on the basis of multivariate analysis of 2-year nursery data. (Wells 1964a, 1964b). A predominately discontinuous genetic variation pattern was revealed between and within the two varieties. Two ecotypes were recognized within the typical variety, *P. p.* var. *ponderosa*: the California ecotype, including progenies from California to the crest of the Sierra Nevadas and Williamette Valley, Oreg.; and the Northern Plateau ecotype, including progenies from northeastern California and the Pacific Northwest to southern British Columbia and western Montana. Three ecotypes were recognized within the interior variety, *P. p.* var. *scopulorum*: the Northern Interior ecotype (Black Hills of South Dakota, Nebraska, and central Montana); the Central Interior ecotype (northern New Mexico, Colorado, and Utah); and the Southern Interior ecotype (Arizona and southern New Mexico).

The most distinct features of the genetic variation pattern of ponderosa pine are that the major variation was ecotypic and that variation within ecotypes, in most cases, seemed to be random. The 8-year data of the above progenies in three test plantations in southern Michigan confirmed the essential distinctions between the varieties and ecotypes, but the relative growth rate of the progenies had changed (Wright *et al* 1969). The progenies of California origin were characterized by rapid first-year height growth. Seedlings from the Southern Interior ecotype (southern New Mexico and Arizona) were the tallest seedlings in the first 2 years. At 8 years, the Pacific Northwest trees were tallest in all three Michigan test plantations. This was primarily because of severe winter injury to California trees and slight winter injury to Arizona-New Mexico origins.

Differences in root growth was found to be related to geographic seed origin in the 3-provenance (Arizona, California, and South Dakota) study of Larson (1967) and the 10-provenance (Arizona, California, Nevada, Oregon, and Wyoming) study of Jenkinson (1976). Among the 10 population samples of ponderosa pine four district seasonal patterns of root-growth capacity are evident. They varied from a single peak in late fall for population samples from eastern Nevada and the Sierra Nevada of California to the bimodal pattern of Wyoming seed origin with highs in late fall and midwinter. These latent patterns develop during the fall and winter while there is no visible growth on seedlings in the nursery.

Read's rangewide 80-seed source ponderosa pine provenance study included 71 population samples that are east of the Continental Divide from Montana and North Dakota south to New Mexico. It is a most comprehensive study, especially for the Rocky Mountain variety, *Pinus ponderosa* var. *scopulorum.* This study was based on a series of multivariate discriminant analysis of 13 seeds and seedling characteristics. The 2-cluster analysis confirmed the primary division of *Pinus ponderosa* var. *ponderosa* and *P. p.* var. *scopulorum.* Seven "clusters" were recognized among the population samples of *P. p.* var. *scopulorum* east of the Continental Divide (Read 1976[4]).

This discrete pattern of geographic variation is also reflected in the turpentine composition (Mirov 1961). Myrcene was found in all parts of the natural range except Colorado and the Black Hills. Limonene, a monocyclic terpene found in many widespread areas, is accompanied by another monocyclic terpene, terpinolene, in southwestern Idaho, southeastern Wyoming, and central Montana, but is replaced by terpinolene in central Colorado and the Black Hills. There is, however, considerable tree-to-tree variation in the monoterpene composition of ponderosa pine located in the same geographic area, as evidenced by Smith's studies (1964a, 1964b) in California. Differences attributable to variation within the tree and seasonal variation were only slight.

Selection of Geographic Seed Source

In recognition of the importance of proper seed sources, seed collection zones were adopted and seed production areas of ponderosa pine established in the Western States (Fowells 1946, Roy 1955, Krugman 1965). The genetic basis of this practice was the maxim, "Local seed source is the safest if not necessarily the best." This general policy was supported by early provenance observations.

In the 1910 three-seed source test at Pikes Peak, the "local" Pike National Forest ponderosa pine seed source was better than those from southern Idaho and Coconino, Ariz. Local seed source germinated best and produced the hardiest seedlings (Hayes 1913). Higgins (1927) reported that nursery stock of indigenous Pine Ridge Nebraska origin produced the best result in Nebraska. Even in the first-year seedlings, indigenous seed source was noticeably larger and sturdier than the closest "nonlocal" seed source from the Black Hills of South Dakota. Austin (1932) reported that of all the progenies tested, the most vigorous strain was found in the "local" Eldorado County. Roeser (1926) concluded that, for all practical purposes, seed collections for any locality should be confined to local varieties, and that for the present it is best to confine seed collection to localities relatively close to the point of use.

Rangewide studies, however, showed that "local" ponderosa pine seed sources closest to the planting site were not always the best in growth. Ten-year growth of two seed sources in a Nebraska test plantation showed that the seed source farther away from the planting site was taller than the nearer source (Read 1966). In the 1926 10-seed source test of Oregon and Washington (Weidman 1939, Munger 1947, Squillace and Silen 1962), no seed source that was closest to the testing site was the best in height growth in any of the five plantations. In general, each seed source tended to perform consistently in spite of the great differences among site conditions. In all five plantations, four of the ten seed sources were consistentaly better than average, and three were consistently poorer. The statistical test of differences among seed sources in all five plantations revealed definite effect of inheritance in height growth.

In the 20-seed source test of Priest River, the 40-year height of the "local" seed source of Kaniksu National Forest (49.2 feet, 15 m), where the test plantation was located, was surpassed by those of Lolo (55.7 ft, 17 m), Umatilla (50.8 ft, 15.5 m), and Colville (49.4 ft, 15.1 m). In survival, the Kaniksu seed source (46 percent) was surpassed by Colville (56 percent) and Umatilla (48 percent). The better ponderosa pine seed sources are more than 100 miles (161 km) away from the testing site, and the altitude of Umatilla seed source (3,500 ft, 1,067 m) is 900 feet (274 m), higher than that of the local Kaniksu seed source (2,600 feet, 792 m). The 40-year data suggested that inclusion of a broad geographic base in initial selection is advisable when considering a selective breeding program.

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[4] Read, R. A. 1976. Genetic variation in 3-year-old seedlings of 80 provenances of ponderosa pine. (Unpublished manuscript.)

Ponderosa pine has been commonly used in forest planting outside of its natural range in North America and other continents. For forest planting in southern Michigan, Wells (1964a) concluded that the Southern Interior ecotype (southern New Mexico and Arizona) seemed to be most promising. In the first 2 years, progenies from this general region were the tallest in height growth, and very frost resistant. They were also characterized by a very deep root system. After outplanting in southern Michigan, however, the Arizona-New Mexico sources suffered winter injury and a reduction in growth. At age 8 they are among the leaders but not the tallest. The tallest trees in all three southern Michigan plantations at age 8 are sources of the North Plateau ecotype (British Columbia, western Montana, eastern Washington, eastern Oregon, and extreme northeast California).

Seedlings used in the 80-provenance, 3-year growth analysis in Nebraska (Read 1976[3]) were included in the 75-provenance test in the Black Hills, S. Dak. (Van Duesen 1974), and the 78-provenance test in east-central Kansas (Deneke and Read 1975). Of all the 75 population samples tested in the Black Hills, 5-year results showed that trees from no other provenance survived significantly better or grew significantly taller than trees from the Black Hills. The poor survival and growth of trees from the Bitterroot Valley of western Montana are in contrast to the generally favorable performance achieved in the 8-seed source test in the Denbigh Experiment Forest, N. Dak. (Conley *et al* 1965). In east-central Kansas, survival was lowest in sources from west of the Continental Divide and from the southern Rocky Mountains.

Six years after field planting, survival of trees derived from natural stands in southeastern Montana, eastern Wyoming, North Dakota, South Dakota, eastern Colorado, and Nebraska was generally very good. The exception was a population sample from central Nebraska, the provenance nearest to the Kansas plantation site. Of the variables analyzed—latitude, elevation, mean annual precipitation, mean annual temperature, and length of growing season—only elevation was significantly (inversely) associated with growth, accounting for approximately 25 percent of the source-growth variation.

In New Zealand, 12 seed sources of ponderosa pine were test planted in 1929. These were population samples from some of the same general geographic areas included in the 10-seed source Oregon-Washington experiment and in the 20-seed source Priest River experiment. Of the 12 seed sources tested for planting in New Zealand, Eldorado, and Sierra sources from the Pacific slope of California outperformed all the seven sources from inland Pacific Northwest in 25-year height growth. Trees from the Rocky Mountain regions (Pike, Lincoln, and Santa Fe) were the slowest growers in the New Zealand test. The 25-year height growth in New Zealand, in comparison with measurements of the two tests in North America, showed that trees from similar geographic sources grew at similar rates in Idaho, Oregon, and Washington and on the Kaingaroa State Forest of New Zealand. This similarity is striking. Trees of similar sources seldom varied as much as 10 percent (Moore 1944, Weston 1957, Squillace and Silen 1962).

Genetic Variation Within Local Populations

A provenance test involving 13 population samples from the Clearwater River drainage in northern Idaho was planted in 1961 on two sites by the Potlatch Corporation. Because of the blister rust epidemic affecting western white pine (*Pinus monticola*), the purpose of this test was to explore alternative pine species for reforestation. At age 16, genetic variation among provenances was apparent for tree height, diameter, and branch numbers. The variation among provenances in growth rate was found to be inversely correlated with variation for strength to withstand snow accumulation. The result indicated that the provenances are sufficiently heterogeneous to produce potentially adaptable and desirable seed for reforestation (Rehfeldt and Cox 1975).

The selection and utilization of the best progenies in the natural population within a geographic area were the basic approaches of the cooperative ponderosa pine improvement program for southern Idaho and as a similar program for the Inland Empire Region that includes northern Idaho and adjacent western Montana and eastern Washington. Open-pollinated progenies from selected natural stands within the general area were tested on different sites where the selected progenies are to be planted. The superior parent trees identified by their progeny performance and the stands of superior trees will be managed to produce genetically better seeds in commercial quantities for local use (Wang 1967).

The 1964 southern Idaho seed orchard project included open-pollinated progenies of 271 parent trees from 37 natural stands in 6 countries within an elevation range of 3,200 to 6,500 ft (975 to 1,981 m). They were field tested in four 13-acre (5 ha) progeny-test seed orchards at different elevations, from 3,700 to 5,350 ft (1,128 to 1,631 m). In the second phase of this project, seedlings of 338 half-sib families were rasied in 1974. The Inland Empire seed orchard project included 460 open-pollinated progenies from 92 natural stands and outplanted in 1974 and 1975 in 10 progeny-provenance plantations in northern Idaho, western Montana, and eastern Washington.

One-year and 2-year seedling height in the four-replicated seed beds (fig. 5) (Wang and Patee 1974), and the 5-year, 8-year, and 12-year height from seed of the progenies at the four test sites (Wang and Patee 1976, Wang 1976[5]) statistically proved highly significant among-family and among-stand differences. The site x progeny interaction was highly significant at the four test sites: 48.7 and 58.2 percent of total variance in 5-year height and 46.3 to 49.9 percent of total variance in 12-year height were associated with stands; 19.5 to 25.2 percent of the total variance in 5-year height and 11.5 to 15.8 percent of the total variance in 12-year height were associated with progeny families.

The within-stand, among-family differences at the four test sites were significant in 3 to 8 of the 35 multitree stands at the 5-year stage, and were significant in only one of the 35 stands at the 12-year stage. This was a drastic change in comparison with the 1-year and 2-year seedlings, where within-stand, among-family differences were significant in 31 to 32 of the 35 stands. Beginning from the 5-year stage, a distinct pattern of population structure became evident. There was more variation among stands than there was variation among mother trees within stands. There was no significant difference among progenies from different age classes of trees superimposed upon the same stand by natural regeneration. And in a relative sense, the half-sib families from a common natural stand (i.e., a small panmictic population) were essentially uniform. Similar results were reported from among physiographic regions and within-stand studies of loblolly pine (Barber 1966, Wells and Switzer 1971, LaFarge 1974).

In seed characteristics, the among-stand seed weight differences are statistically very significant. The among-family seed length and seed width differences are highly significant, but their among-stand differences are not. The 1-year seedling height was positively correlated with seed size and seed weight, but the partial correlations of 2-year, 5-year, 8-year, and 12-year heights with the above seed characteristics were not significant.

Progeny family height was used as an indication of its vigor and general adaptability. In three of the four test plantations, samples of ordinary planting stock raised at the same nursery from bulked local seed sources for commercial planting at the Payette National Forest (PNF, Control 777) and Boise National Forest (BNF, Control 888), where the progeny-test plantations were located and where the genetically improved seeds will be used, were included as control plots in all the replicates. The differences in height between the ordinary planting stock and the best progeny family,

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[5] Wang, C. W. 1976. Unpublished data.

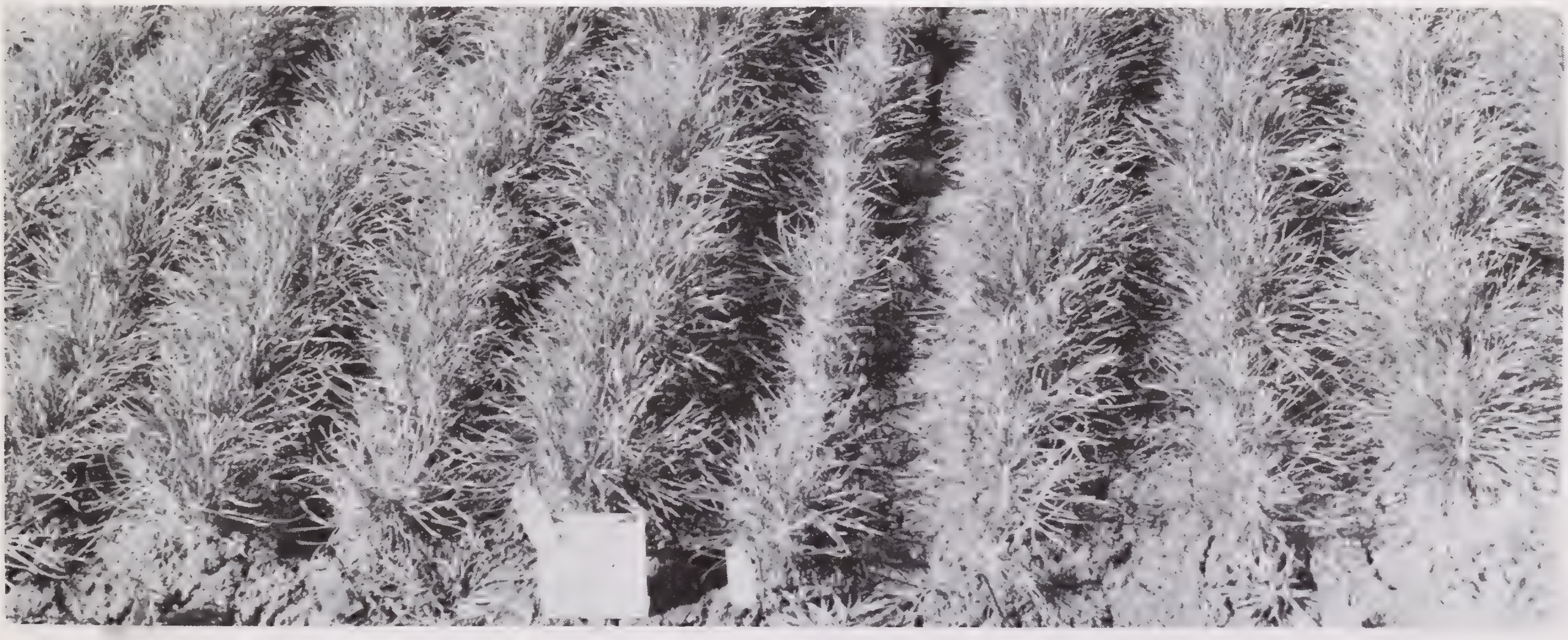

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Figure 5.—Progeny test of ponderosa pine. Highly significant differences among mother trees and among stands were demonstrated by the 2-year seedlings of 271 open-pollinated families (Wang and Patee 1974).

the best stand, and the 271 tested families, as expressed by their ratios, are presented in table 1.

The superior parent trees, as identified by their superior progeny performance, and the superior stands, where the superior parent trees are located, produced seedlings that consistently outperformed the controls at the test sites (table 1). The best progeny families were 44 to 51 percent taller at age 12 from seed than the ordinary planting stock of the same age planted at the same time at the same site. In the natural population, the parent trees of the fast-growing progenies were not distributed at random but were found to be concentrated in certain local populations. For the second phase of the improvement project, additional sample trees from the superior stands and from additional phenotypically desirable stands in their vicinity were included in the progeny test for further evaluation and selection.

Flower and cone production is late in ponderosa pine. Of the four 13-acre (5 ha) progeny-test seed orchards, one cone was produced at age 10 from seed, and no more than 10 cones were produced before age 12. For seed production, however, the superior parent trees and trees in the superior natural stands are in prime seed-production age. The superior parent trees are sample trees of natural stands and are mostly pollinated by neighboring trees. The superior stands are mostly regenerated at the same year from a common general seed source of their neighborhood. The analysis of 5-year, 8-year, and 12-year within-stand variations of 35 natural stands (fig. 6) (Wang and Patee

Table 1.—*Height of 5-year, 8-year, and 12-year open-pollinated progenies compared with ordinary planting stock on three test sites*[1] *on the Payette and Boise National Forests*

Age and Location		Best family		Best stand		Plantation mean	
		Payette N.F.	Boise N.F.	Payette N.F.	Boise N.F.	Payette N.F.	Boise N.F.
5-year	Site 2	1.78		1.45		1.21	
	Site 3	2.03		1.32		1.12	
	Site 4	1.55	1.44	1.26	1.16	1.11	1.03
	Average	1.79	1.76	1.35	1.32	1.15	1.12
8-year	Site 2	1.45		1.17		1.03	
	Site 3	1.51		1.24		.92	
	Site 4	1.53	1.43	1.18	1.11	1.06	1.06
	Average	1.49	1.48	1.20	1.19	1.01	1.01
12-year	Site 2	1.36		1.22		1.00	
	Site 3	1.53		1.13		0.94	
	Site 4	1.66	1.45	1.29	1.13	1.15	1.00
	Average	1.51	1.44	1.21	1.15	1.03	0.98

[1] Site 2—4,750 ft, 1,448 m; site 3—5,350 ft, 1,631 m; site 4—3,700 ft, 1,128 m.

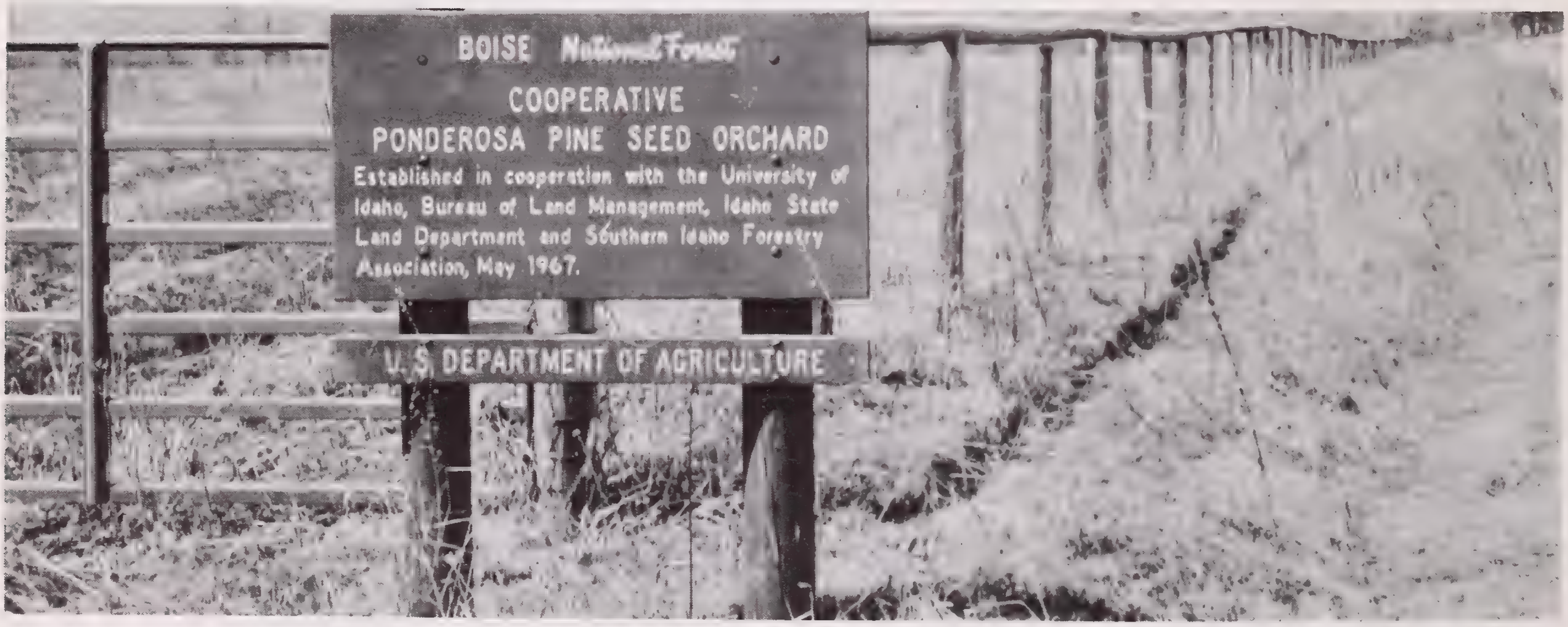
BOISE National Forest
COOPERATIVE
PONDEROSA PINE SEED ORCHARD
Established in cooperation with the University of Idaho, Bureau of Land Management, Idaho State Land Department and Southern Idaho Forestry Association, May 1967.
U.S. DEPARTMENT OF AGRICULTURE

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Figure 6.—A ponderosa pine progeny test seed orchard of the University of Idaho Cooperative Southern Idaho ponderosa pine improvement program (Wang and Patee 1976).

1976) confirmed the essential uniformity of the progeny parents, including the seed parents and the pollen parents. On the basis of their progeny performance, the superior seed trees and hundreds of trees of the superior stands can be used for production of genetically superior seeds in commercial quantities before seeds are available from the seed orchards. The seed orchard will be created by selective thinning of the progeny test plantations. Selection will be made among the half-sib families and among individuals within the families (Wang 1967).

Two experiments on within-family selection were made on ponderosa pine seedlings (Callaham and Duffield 1963, Callaham and Hasel 1958, 1961). In the low-intensity selection of about 20 percent, or the best of four to six seedlings, seed size effects were reduced by using only seed of a single size grade. Seedlings having longest epicotyls after 75 days in the nursery generally produced taller trees than seedlings with shortest epicotyls at 2, 5, 12, and 20 years, but differences in mean height of trees from these two classes of seedlings were not significant after 2 years. This experiment indicates that within a progeny, epicotyl length after 75 days cannot be used to predict height of ponderosa pines at 12 or 20 years. However, height at 12 and 20 years can be predicted rather well from height at 5 years or later. Height at 5 years predicts about 40 to 60 percent of the variation at 12 years.

In the moderate intensity selection within open-pollinated progenies of 81 seed trees, the best of 16 to 18 seedlings, or the top 6 percent, was selected. Seedlings chosen at this intensity did show significant differences in height, diameter, and stem volume at 15 years. The seedlings were selected as tallest, shortest, and average. The three classes of seedlings retained their ranking at 15 years with statistically significant distinction among tallest, shortest, and average.

In diameter growth, it was demonstrated that phenologically selected parents from a local population produced inherently different progeny families. Stocky parents produced seedlings that were stockier than progenies from slender parents. Silen and Rowe (1971) selected seven pairs of adjacent open-grown parents in Oregon for their striking phenotypic differences in stem form. The stocky parent trees of the seven pairs were about 30 percent stockier than the slender parent trees, and at age 3, progeny families of the stocky parents were about 22 percent stockier than the slender tree progenies.

Interspecific Hybridization

One source of the great potential variability in ponderosa pine is its broad pattern of crossability. Ponderosa pine crosses with *P. montezumae*, and *P. montezumae* crosses with Mexican pines of the *P. pseudostrobus* complex. It is reasonable to assume that directly and indirectly no less than 30 species and varieties of *Diploxylon* pines of western North America and Mexico are potentially involved in hybridization with ponderosa pine.

The natural range of ponderosa pine and Jeffrey pine overlap broadly in California, but natural ponderosa pine × Jeffrey pine hybrids are rare. In general, ponderosa pine grows at lower elevations than Jeffrey pine. The difference in flowering time is an additional breeding barrier. Haller (1962) found that seed set and survival of hybrids were low in the mixed stands of ponderosa pine and Jeffrey pine where natural hybridization and back crossing of the hybrids were observed. He concluded that gene exchange between these two species is very limited.

Introgressive hybridization of ponderosa pine with *Pinus washoensis* was observed in northeastern California (Haller 1961). Washoe pine is confined to a few isolated stands in western Nevada and in adjacent northeastern California. The stands are all above the general altitudinal zone of ponderosa pine. However, Washoe pine also occurs sporadically at lower elevations in northeastern California (Hobard Mills, 5,800 ft) or (1,768 m) where ponderosa pine differs strikingly from nearby populations and displays great variability. Many of the trees in this apparent hybrid swarm are more similar to *Pinus washoensis* than they are to typical ponderosa pine.

In the *Pinus* hybridization program of the Institute of Forest Genetics at Placerville, Calif. ponderosa pine was crossed with a number of hard pine species. Artificial hybrids were obtained in crosses between ponderosa pine and *P. engelmanni*, *P. jeffreyi*, *P. montezumae*, *P. washoensis*, *P. durangensis*, and varieties of ponderosa pine, var. *scopularum*, and var. *arizonica*. Seed set was low in the crosses with Jeffrey pine and *P. durangensis*. Ponderosa pine was found to be incompatable with *P. coulteri* and hard pines of the Subsection *Australes* of the southeastern States, including *P. echinata*, *P. palustris*, *P. sondereggeri* and *P. taeda* (Righter and Duffield 1951a, Duffield 1952, Duffield and Righter 1953, Liddicoet and Righter 1960, Critchfield 1966).

Improvement in form and size of seedlings and in rate of early plantation growth has been affected by crossing ponderosa pine with Apache pine (*P. engelmanni*) and Montezuma pine (*P. montezumae*) (Righter and Duffield 1951b, Righter 1955). The ponderosa pine × Apache pine hybrid outgrows ponderosa pine in both height and diameter in the ponderosa pine habitat. The ponderosa pine × Montezuma pine hybrid outgrows the ponderosa × Apache hybrid by a considerable margin in height, but it lacks the early diameter growth. The trispecies hybrid produced by crossing ponderosa × Apache hybrid with Montezuma pine equals the ponderosa × Montezuma hybrid (Righter 1955). A distinct feature of the ponderosa × Apache hybrid is the development of a long taproot in the seedling stage. The rapid penetration of a prodigious root is of crucial importance for survival in summer drought areas.

The ponderosa pine × Apache pine hybrid was found to be as susceptible to killing by pine reproduction weevil (*Cylindrocopturus eatoni* Buch.) as are ponderosa pine and Jeffrey pine, but Coulter pine was completely resistant to this insect under forced attacks (Miller 1950). Interspecific crossings were made at the California Institute of Forest Genetics to introduce into the weevil-susceptible ponderosa pine, Jeffrey pine, and ponderosa × Apache pine hybrid the resistance possessed by *P. coulteri*. Ponderosa pine does not cross with Coulter pine, but *P. coulteri* was able to cross with *P. jeffreyi* and *P. ponderosa* with *P. jeffreyi* and the *P. jeffreyi* × *P. coulteri* hybrid (Zobel 1951, Libby 1958, Critchfield 1966). The cross between natural hybrids *Jeffreyi* × *ponderosa* and *Jeffreyi* × *coulteri* has been tried without success (Righter and Duffield 1951a). The backcross of natural Jeffrey × Coulter hybrids to Jeffrey was successful, however, and exhibited a high level of resistance under forced attacks (Miller 1950, Smith 1960) and in field tests (Hall 1959). This resistance led the Forest Service to start large-scale production of the backcross hybrids (Libby 1958).

In general, our current knowledge of the genetics of ponderosa pine has demonstrated that genetic improvement of this economically important tree can be obtained in two basic approaches. With the wide range of variation in the natural population, substantial improvement can be expected by the utilization of desirable natural variants in inter- and intra-ecotypic selections (Wang 1967). With its broad pattern of crossability, valuable artificial variants of ponderosa pine and its hybrids can be created through a large combination of potentially possible interecotype and interspecies crosses and their backcrosses with species and varieties in the Subsection *Ponderosae*, and indirectly through *P. jeffreyi*, with pines of the Subsection *Sabinianae*, the big-cone pine group (Critchfield 1966).

LITERATURE CITED

Adams, L.
1950. Consumption of ponderosa pine seed by small mammals. USDA For. Serv. North. Rocky Mt., For. and Range Exp. Stn., Res. Note No. 80. 4 p.

Adams, L.
1955. Pine squirrels reduce future crops of ponderosa pine cones. J. For. 53: 35.

Austin, L.
1932. Hereditary variation in western yellow pine. Madroño 2: 62–63.

Axelrod, D. I.
1939. A Miocene flora from the western border of the Mohave Desert. Carnegie Inst. Wash. Publ. No. 516. 129 p.

Axelrod, D. I.
1956. Mio-Pliocene floras from west-central Nevada. Calif. Univ. Publ., Geol. Sci. 33. 322 p.

Axelrod, D. I.
1966. The Eocene Copper Basin flora of northeastern Nevada. Univ. Calif. Publ. Geol. Sci. 59. 83 p.

Baker, F. S., and C. F. Korstian.
1931. Suitability of brushlands in the Intermountain Region for the growth of natural or planted western yellow pine forests. U.S. Dep. Agric., Tech. Bull. No. 256. 83 p.

Barber, J. C.
1966. Variation among half-sib families from three loblolly pine stands in Georgia. Ga. For. Res. Counc., Res. Pap. 37. 5 p.

Bates, C. G.
1927. Varietal differences. J. For. *25*: 610.

Boe, K. N.
1954. Periodicity of cone crops for five Montana conifers. Mont. Acad. Sci., Proc. *14*: 5–9.

Buchholz, J. T.
1918. Suspensor and early embryo of *Pinus*. Bot. Gax. *66*: 185–228.

Buchholz, J. T.
1922. Developmental selection in vascular plants. Bot. Gaz. *73*: 249–286.

Buchholz, J. T.
1931. The pine embryo and the embryos of related genera. Trans. I11. Acad. Sci. *23*: 117–125.

Buchholz, J. T.
1946. Volumetric studies of seeds, endosperms, and embryos in *Pinus ponderosa* during embryonic differentiation. Bot. Gaz. *108*: 232–244.

Buchholz, J. T., and M. L. Stiemert.
1946. Development of seeds and embryos in *Pinus ponderosa* with special reference to seed size.

Trans. I11. Acad. Sci. *38*: 27–50.

Callaham, R. Z.
1960. Map of the distribution of ponderosa pine. U.S. Dep. Agric., For. Serv.

Callaham, R. Z., and J. W. Duffield.
1963. Height of selected ponderosa pine seedlings during 20 years. For. Genet. Workshop. Proc. 1962. S.F.T.I. Comm. Publ. *22*: 10–1.

Callaham, R. Z., and A. A. Hasel.
1958. Height growth of ponderosa pine progenies. Proc. Soc. Am. For., 1957: 61–62.

Callaham, R. Z., and A. A. Hasel.
1961. *Pinus ponderosa* height growth of wind pollinated progenies. Silv. Genet. *10*: 33–42.

Callaham, R. Z., and A. R. Liddicoet.
1961. Altitudinal variation at 20 years in ponderosa and Jeffrey pines. J. For. *59*: 814–820.

Callaham, R. Z., and W. Metcalf.
1959. Altitudinal races of *Pinus ponderosa* confirmed. J. For. *57*: 500–502.

Chaney, R. W.
1936. Plant distribution as a guide to age determination. Wash. Acad. Sci. J. *26*: 313–324.

Chaney, R. W., C. Coudit, and D. I. Axelrod.
1944. Pliocene floras of California and Oregon. Carnegie Inst. Wash. Publ. No. 553.

Conkle, T.
1973. Growth data for 29 years from the California elevational transect study of ponderosa pine. For. Sci. *19*: 31–39.

Conley, W. T., D. H. Dawson, and R. B. Hill.
1965. The performance of eight seed sources of ponderosa pine in the Denbigh Experimental Forest, N. Dak. U. S. Dep. Agric., For. Serv., Res. Note LS-71. 4 p.

Crafts, E. C.
1958. A summary of the timber resources review in timber resources for America's future. U.S. Dep. Agric., For. Resour. Rep. No. 14.

Critchfield, W. B.
1966. Crossibility and relationships of the California big-cone pines. Joint Proceedings 2d Genetics Workshop of Society American Forestry and the 7th Lake States Forest Tree Improvement Conference 1965. USDA For. Serv. Res. Pap. NC-6. p. 36–44.

Critchfield, W. B., and G. L. Allenbaugh.
1969. The distribution of *Pinaceae* in and near northern Nevada. Madroñe *20*: 12–26.

Critchfield, W. B., and E. L. Little.
1966. Geographic distribution of the *Pinus* of the world. U. S. Dep. Agric., Misc. Publ. 991. 97 p.

Cumming, W. C., and F. I. Righter.
1948. Methods used to control pollination of pines in the Sierra Nevada of California. U. S. Dep. Agric. Circ. 792. 18 p.

Curtis, J. D.
1955. Effects of origin and storage method on the germination capacity of ponderosa pine seed. USDA For. Serv. Intermt. For. and Range Exp. Stn., Res. Note No. 26. 5 p.

Curtis, J. D., and D. W. Lynch.
1957. Silvics of ponderosa pine. USDA For. Serv. Intermt. For. and Range Exp. Stn. Misc. Publ. No. 12. 37 p.

Dahms, W. G., and J. W. Barrett.
1975. Seed production of Central Oregon ponderosa and lodgepole pines. USDA For. Serv., Res. Pap. PNW-191. 13 p.

Daubenmire, R. F.
1950. A comparison of season of cambial growth in different geographic races of *Pinus ponderosa*. Bot. Gaz. *112*: 182–188.

Day, B. B., and L. Austin.
1939. A 3-dimensional lattice design for studies in forest genetics. J. Agric. Res. *59*(2): 101–120.

Deneke, F. J., and R. A. Read.
1975. Early survival and growth of ponderosa pine provenances in east-central Kansas. USDA For. Serv., Res. Note RM-297. 4 p.

Duffield, J. W.
1947. Dates and places of pollen collection by the Institute of Forest Genetics. USDA For. Serv., Calif. For. and Range Exp. Stn., Res. Note No. 54. 5 p.

Duffield, J. W.
1952. Relationships and species hybridization in genus *Pinus*. Silv. Genet. *2*: 93–96.

Duffield, J. W.
1953. Pine pollen collection dates—annual and geographic variation. USDA For. Serv. Calif. For. and Range Exp. Stn., Res. Note No. 85. 9 p.

Duffield, J. W.
1954. Studies of extraction, storage and testing of pine pollen. Z. für Forstgenetick und Forstpflanzenzüchtung. *3*(2): 39–45.

Duffield, J. W., and F. I. Righter.
1953. Annotated list of pine hybrids made at the Institute of Forest Genetics. USDA For. Serv., Calif. For. and Range Exp. Stn., Res. Note No. 86. 9 p.

Duffield, J. W., and R. Z. Callaham.
1959. Deep-freezing pine pollen. Silv. Genet. *8*: 22–24.

Echols, R. M., and M. T. Conkle.
1971. The influence of plantation and seed-source elevation on wood specific gravity of 20-year-old ponderosa pine. For. Sci. *17*: 388–394.

Echols, R. M.
1973. Effects of elevation and seed source on tracheid length in young ponderosa pine. For. Sci. *19*: 46–48.

Fechner, G. H., and R. W. Funsch.
1966. Germination of blue spruce and ponderosa pine pollen after eleven years of storage at 0° to 4° C. Silv. Genet. *15*: 164–166.

Fowells, H. A.
1946. Forest seed collection zones in California. USDA For. Serv., Calif. For. and Range Exp. Stn., Res. Note No. 51. 5 p.

Fowells, H. A., and G. H. Schubert.
1956. Seed crops of forest trees in the pine region of California. U. S. Dep. Agric., Tech. Bull. No. 1150. 48 p.

Gaussen. H.
1960. Les gymnospermes actuelles et fossiles. Fasc. VI, Chap. XI, Genre *Pinus*. Toulouse.

Gifford, E. M., and N. T. Mirov.
1960. Initiation and ontogeny of the ovulate strobilus in ponderosa pine. For. Sci. *6*: 19–25.

Graham, B. F., and F. H. Borman.
1966. Natural root grafts. Bot. Rev. *32*: 255–292.

Gravatt, A. R., D. H. Latham, L. W. R. Jackson, G. Y. Young, and W. C. Davis.
1940. Multiple seedlings of pines and Douglas-fir. J. For. *38*: 818.

Haagen-Smit, A. J., C. T. Redeman, T. H. Wang, and N. T. Mirov.
1950. Composition of gum turpentines of *Pinus ponderosa*. J. Am. Pharm. Assoc. Sci. Ed. *39*: 260–261.

Haagen-Smit, A. J., T. H. Wang, and N. T. Mirov.
1951. Composition of gum turpentine of pinus XIII. J. Am. Pharm. Assoc. Sci. Ed. *40*: 557–559.

Hall, R. C.
1959. Field tests of the resistance of hybrid pines to

the pine reproduction weevil. USDA For. Serv., Pac. Southwest For. and Range Exp. Stn., Tech. Pap. 33. 21 p.

Haller, J. R.
1959a. The role of hybridization in the origin and evolution of *Pinus washoensis*. Abstr. Proc. 9th Internatl. Bot. Cong. *2*: 149.

Haller, J. R.
1959b. Factors affecting the distribution of ponderosa and Jeffrey pines in California. Madroño *15*(3): 65–71.

Haller, J. R.
1961. Some recent observations on ponderosa, Jeffrey and Washoe pines in northeastern California. Madroño *16*: 126–132.

Haller, J. R.
1962. Variation and hybridization in ponderosa and Jeffrey pines. Univ. Calif. Publ. Bot. *34*(2):123–166.

Haller, J. R.
1965a. *Pinus washoensis* in Oregon: taxonomic and evolutionary implications. Am. J. Bot. *52*: 646.

Haller, J. R.
1965b. The role of 2-needle fascicles in the adaptation and evolution of ponderosa pine. Brittonia *17*: 354–382.

Hansen, H. P.
1942. The influence of volcanic eruptions upon post-Pliocene forest succession in central Oregon. Am. J. Bot. *29*: 214–219.

Hansen, H. P.
1947. Post-glacial vegetation of the northern Great Basin. Am. J. Bot. *34*: 164–171.

Hansen, H. P.
1949. Post-glacial forests in west central Alberta, Canada. Torrey Bot. Club Bull. *76*: 278–289.

Hanover, J. W.
1963. Geographic variation in ponderosa pine leader growth. For. Sci. *9*: 86–95.

Harlow, W. M., and E. S. Harrar.
1958. Textbook of dendrology (4th ed.) McGraw-Hill, N.Y.

Hayes, W. D.
1913. Effect of source of seed on results in yellow pine reforestation, Fremont Exp. Stn. USDA Rev. For. Serv. Invest. *2*: 53–57.

Herman, R. C., (ed).
1970. Regeneration of ponderosa pine. Paper 681, Sch. For., Oreg. State Univ., Corvallis. 125 p.

Higgins, Jay.
1927. Facts and figures regarding the Nebraska planting project. J. For. *25*: 1023–1030.

Howe, Virgil K.
1962. Culture of excised embryos of *Pinus ponderosa*. Iowa Acad. Sci., Proc. *69*: 137–142.

Iloff, P. M., and N. T. Mirov.
1954. Composition of gum turpentines of pines XIX. A report of *Pinus ponderosa* from Arizona, Colorado, South Dakota, and northern Idaho. J. Am. Pharm. Assoc. Sci. Ed. *43*: 373–378.

Jenkinson, J. L.
1976. Seasonal patterns of root growth capacity in western yellow pines. *In* America's renewable resource potential-1975: the turning point. Proc., 75th Natl. Conv., Soc. Am. For. Wash. D.C. 1975. p. 445–463.

Kempff, G.
1928. Nonindigenous western yellow pine plantations in northern Idaho. Northwest Sci. *2*: 54–58.

Krugman, S. L.
1965. A seed production area and a seed orchard in California—a progress report. 4th Calif. For. and Soil Fert. Conf. Proc. 1965. p. 69–76. Calif. Fert. Assoc. Redding.

Krugman, S. L., and T. W. Koerber.
1969. Effect of cone feeding by *Leptoglossus occidentalis* on ponderosa pine seed development. For. Sci. *15*: 104–111.

LaFarge, T.
1974. Genetic variation among and within three loblolly pine stands in Georgia. For. Sci. *20*: 272–275.

Lanner, R. M.
1961. Living stumps in Sierra Nevada. Ecology *42*: 170–173.

Larson, M. M.
1966. Racial variation of ponderosa pine at Fort Valley, Ariz. USDA For. Serv., Res. Note RM-73 7 p.

Larson, M. M.
1967. Effect of temperature on initial development of ponderosa pine seedlings from three sources. For. Sci. *13*: 286–294.

Lemmon, J. G.
1890. Revision of broken cone pines. Calif. State Bd. For. 3rd Bien. Rep. (889–90) 196–201.

Lesquereux, L.
1883. Contributions of the fossil flora of the Western Territories. III. The Cretaceous and Tertiary floras. U.S. Geol. of the Territories Rep. *8*: 283 p.

Libby, W. J.
1958. The backcross hybrid Jeffrey × (Jeffrey × Coulter) pine. J. For. *56*: 840–842.

Liddicoet, A. R., and F. I. Righter.
1960. Trees of the Eddy Arboretum. USDA For. Serv., Pac. Southwest For. and Range Exp. Stn., Misc. Pap. 43. 41 p.

Little, E. L.
1950. Southwestern trees—a guide to the native species of New Mexico and Arizona. U. S. Dep. Agric., Agric. Handb. 9. 109 p.

MacGinitie, H. D.
1953. Fossil plants of the Florissant Beds, Colo. Carnegie Inst. Wash. Publ. No. 599.

Maguire, W. P.
1956. Are ponderosa pine crops predictable? J. For. *54*: 778–779.

Maki, T. E.
1940. Significance and applicability of seed maturity indices for ponderosa pine. J. For. *38*: 55–60.

Mehra, P. N., and T. N. Khoshoo.
1956. Cytology of conifers, I. J. Genet. *54*: 165–185.

Miller, J. M.
1950. Resistence of pine hybrids to the reproduction weevil. USDA For. Serv., Calif. For. and Range Exp. Stn., Res. Note 68. 17 p.

Mirov, N. T.
1929. Chemical analysis of the oleoresins as a means of distinguishing Jeffrey pine and western yellow pine. J. For. *27*: 176–187.

Mirov, N. T.
1938. Phylogenetic relations of *Pinus jeffreyi* and *P. ponderosa*. Madroño *4*: 169–171.

Mirov, N. T.
1940. Tested methods of grafting pines. J. For. *38*: 768–777.

Mirov, N. T.
1942. Possibility of simple biochemical tests for differentiation between species of genus *Pinus*. J. For. *40*: 953–954.

Mirov, N. T.
1944. Experiments in rooting pines in California. J. For. *42*: 199–240.

Mirov, N. T.
1951a. Composition of gum turpentine of pines. A

report on *Pinus ponderosa* from Utah. J. Am. Pharm. Assoc. Sci. Ed. *40*: 410–413.

Mirov, N. T.
1951b. A report on *Pinus echiniata*, *P. rigida*, and *P. ponderosa* from the composition of gum turpentines of pines XIV. J. Am. Pharm. Assoc. Sci. Ed. *41*: 673–676.

Mirov, N. T.
1954. Apache pine and its relationship to ponderosa pine. Madroño *12*: 251–252.

Mirov, N. T.
1956. Photoperiod and flowering of *Pinus*. For. Sci. *2*: 328–332.

Mirov, N. T.
1961. Composition of gum turpentines of pines. U. S. Dep. Agric., Tech. Bull. 1239. 158 p.

Mirov, N. T.
1967. The genus *Pinus*. Ronald Press, N. Y. 602 p.

Mirov, N. T., J. W. Duffield, and A. R. Liddicoet.
1952. Altitudinal races of *Pinus ponderosa*— a 12-year progress report. J. For. *50*: 825–831.

Mirov, N. T., and W. P. Stockwell.
1939. Colchicine treatment of pine seeds. J. Heredity *30*: 389–390.

Moore, A. M.
1944. *Pinus ponderosa* Douglas, comparison of various types grown experimentally on Kaingaroa State Forest, N. Zealand. J. For. *5*: 42–49.

Mowat, E. L., and R. R. Silen.
1957. A test of grafting ponderosa pine. USDA For. Serv., Pac. Northwest For. and Range Exp. Stn., Res. Note No. 155. 5 p.

Munger, T. T.
1947. Growth of ten regional races of ponderosa pine in six plantations. USDA For. Serv., Pac. Northwest For. and Range Exp. Stn., Res. Note 39. 4 p.

Namkoong, G., and M. T. Conkle.
1976. Time trends in genetic control of height growth in ponderosa pine. For. Sci. *22*: 2–12.

Parks, G. K.
1969. Field grafting ponderosa pine in the California region. U. S. Dep. Agric., For. Serv. (Abstract). Proc. Annual Meeting West. For. Gen. Assoc., Placerville, Calif. 1969.

Parks, G. K.
1974. Field grafting California ponderosa pine. Tree Plant. Notes *25*(3): 12–14.

Pearson, G. A.
1912. The influence of age and condition of the tree upon seed production in western yellow pine. U. S. Dep. Agric., Circ. 196. p. 11.

Pearson, G. A.
1931. Forest types in the Southwest as determined by climate and soil. U. S. Dep. Agric., Tech. Bull. 247. p. 144.

Pearson, G. A.
1950. Management of ponderosa pine in the Southwest. U. S. Dep. Agric. Monogr. 6. 218 p.

Pemberton, C. C.
1920. Living stumps of trees. Am. For. *26*:614–616.

Pike, G. W.
1927. The relation of the viability of seed to the age of the parent tree. Idaho For. *9*: 17–18.

Read, R. A.
1966. Ten-year growth of two sources of large grade ponderosa pine transplants in Nebraska. USDA For. Serv., Rocky Mt. Stn., Res. Note RM-70. 3 p.

Rehfeldt, G. E., and R. G. Cox.
1975. Genetic variation in a provenance test of 16-year-old ponderosa pine. USDA For. Ser. Res. Note INT-201. 7 p.

Righter, F. I.
1936. Early flower production among the *Pinus*. J. For. *37*: 935–938.

Righter, F. I.
1955. Possibilities and limitations of hybridization in *Pinus*. Third South. Conf. For. Tree Improv. Proc. 1955: 54–63.

Righter, F. I., and J. W. Duffield.
1951a. Interspecies hybrids in pines. J. Heredity *42*: 75–80.

Righter, F. I., and J. W. Duffield.
1951b. Hybrids between ponderosa and Apache pines. J. For. *49*: 345–349.

Roeser, J.
1926. The importance of seed source and the possibilities of forest tree breeding. J. For. *2*: 38–51.

Roeser, J.
1941. Some aspects of flower and cone production in Ponderosa pine. J. For. *39*: 534–536.

Roy, D. F.
1955. Oregon limits of California tree seed collection zones. USDA For. Serv. Calif. For. and Range Exp. Stn., Res. Note 93. 3 p.

Sax, K., and H. J. Sax.
1933. Chromosome number and morphology in the conifers. Arnold Arbor. J. *14*: 356–375.

Saylor, L. C., and B. W. Smith.
1966. Meiotic irregularity in species and interspecific hybrids of *Pinus*. Am. J. Bot. 453–468.

Saylor, L. C.
1972. Karyotype analysis of the genus *Pinus*-subgenus *Pinus*. Silv. Genet. *21*: 155–163.

Schreiner, E. J.
1937. Improvement of forest trees. Yearb. Agric. U. S. Dep. Agric. 1937: 1242–1279.

Shaw, G. R.
1914. The genus *Pinus*. Arnold Arbor. Publ. No. 5. 96 p.

Shea, K. R.
1965. Patch graft dwarf mistletoe-infected ponderosa pine bark tissues. For. Sci. *11*: 436–437.

Shearer, R. C., and W. C. Schmidt.
1971. Ponderosa pine cone and seed losses. J. For. *69*: 370–372.

Silen, R. R., and K. E. Rowe.
1971. Inheritance of stockiness in ponderosa pine families. USDA For. Serv., Res. Note PNW-166. 12 p.

Smith, R. H.
1960. Resistance of pines to the pine reproduction weevil, *cylindrocopturus eatoni*. J. Econ. Entomol. *53*: 1044–1048.

Smith, R. H.
1964a. Variation in monoterpenes of *Pinus ponderosa* Laws. Science *143:* 1337–1338.

Smith, R. H.
1964b. Variations in the monoterpene composition of ponderosa pine wood oleoresin. USDA For. Serv., Res. Pap. PSW-15, 17 p.

Smith, R. H.
1967. Variations in the monoterpene composition of the wood resin of Jeffrey, Washoe, Coulter and lodgepole pines. For. Sci. *13*: 246–252.

Sorensen, F. C., and R. S. Miles.
1974. Self-pollination effects on Douglas-fir and ponderosa pine seeds and seedlings. Silv. Genet. *23*: 135–138.

Squillace, A. E.
1953. Effect of squirrels on the supply of ponderosa pine seed. USDA For. Serv., Northern Rocky Mt. For. and Range Exp. Stn., Res. Note No. 131. 4 p.

Squillace, A. E., and R. R. Silen.
1962. Racial variation in ponderosa pine. For. Sci. Monogr. 2. 27 p.

Stanley, R. G.
1962. Viable pollen stored 15 years produces unsound seed. Silv. Genet. *11*: 164.

Stanley, R. G., J. Petersen, and N. T. Mirov.
1960. Viability of pine pollen stored 15 years. USDA For. Serv., Pac. Southwest For. and Range Exp. Stn., Res. Note 173. 5 p.

Stanley, R. G., and I. Poostchi.
1962. Endogenous carbohydrates, organic acids, and pine pollen viability. Silv. Genet. *11*: 1–3.

Steinhoff, R. J.
1970. Northern Idaho ponderosa pine racial variation study—50-year results. USDA For. Serv., Res. Note INT-118. 4 p.

Steinhoff, R. J.
1974. Juvenile-mature correlation in ponderosa and western white pine. Proc. Joint IUFRO Meet. S.02.04. 1–3, Sess. IV, Stockholm. p. 243–250.

Stone, E. L.
1974. The communal root system of red pine; growth of girdled trees. For. Sci. *20*: 294–305.

Sudworth, G. B.
1917. The pine trees of the Rocky Mountain Region. U. S. Dep. Agric., Bull. 460. 47 p.

Thimann, K. V., and J. Behnke-Rogers.
1950. The use of auxins in the rooting of woody cuttings. Maria Moore Cabot Found. Publ. No. 1. 344 p.

VanDeusen, J. L.
1974. Five-year results of a ponderosa pine provenance study in the Black Hills. USDA For. Serv., Res. Note RM-278. 4 p.

Wang, C. W.
1967. The genetic improvement of ponderosa pine in Idaho. Univ. of Idaho, For., Wildlife and Range Exp. Stn., Stn. Note 7. 7 p.

Wang. C. W.
1970. Cone and seed production in controlled pollination of ponderosa pine. Univ. of Idaho, For. Wildlife and Range Exp. Stn., Stn. Pap. No. 7. 15 p.

Wang, C. W., and R. K. Patee.
1973. Progeny performance of 271 ponderosa pine parents. 1973 West. For. Genet. Assoc. Symp., Coeur d'Alene, Idaho. 12 p.

Wang. C. W., and R. K. Patee.
1974. Variation in seed characteristics and seedling growth of open pollinated ponderosa pine progenies. Univ. of Idaho, For., Wildlife, and Range Exp. Stn., Stn. Pap. No. 15. 11 p.

Wang., C. W., and R. K. Patee.
1976. Regional variation of ponderosa pine, the five-year result. Univ. of Idaho, For., Wildlife and Range Exp. Stn., Bull. No. 10. 7 p.

Weidman, R. H.
1939. Evidences of racial influence in a 25-year test of ponderosa pine. J. Agric. Res. *59*: 855–887.

Wells, O. O.
1964a. Geographical variation in ponderosa pine, I. The Ecotypes and their distribution. Silv. Genet. *13*: 89–103.

Wells, O. O.
1964b. Geographical variation in ponderosa pine, II. Correlation between progeny performance and the characteristics of the native habitat. Silv. Genet. *13*: 125–132.

Wells, O. O., and G. L. Switzer.
1971. Variation in rust resistance in Mississippi loblolly pine. Proc. 11th South. Conf. Tree Improv. 1971: 25–30.

Weston, G. G.
1957. Exotic forest trees in New Zealand. Paper prepared for the 7th British Commonwealth Forestry Conference, Australia and New Zealand, 1957. New Zealand For. Serv. Bull. 13. 104 p.

Wodehouse, R. P.
1933. Tertiary pollen II. The oil shales of the Eocene Green River formation. Torrey Bot. Club Bull. *60*: 479–524.

Wolfe, J. A.
1964. Miocene floras from Fingerrock, Washington, southwestern Nevada. Geol. Survey Prof. Pap. 454-N. 36 p.

Wolfe, J. A., D. M. Hopkins, and E. B. Leopold.
1966. Tertiary stratigraphy and Paleobotany of the Cook Inlet Region, Alaska. Geol. Survey Professional Pap. 398-A. 29 p.

Wright, J. A., W. A. Lemmien, and J. N. Bright.
1969. Early growth of ponderosa pine ecotypes in Michigan. For. Sci. *15*: 121–129.

Zobel, B.
1951. The natural hybrid between Coulter and Jeffrey pines. Evolution *5*: 405–413.

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